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Vegetation responses to chaining in an isolated remnant in Western Australia's wheatbelt

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Abstract

This study examines secondary succession in an isolated remnant following disturbance by chaining, where a chain suspended by two tractors was drawn along the ground knocking over the vegetation. The disturbance resulted in distinct zones within the chained area (chained and mulched, chained and cleared, and chained with vegetation piles burnt). Two to three years after disturbance distinct assemblages occurred within each zone, with high diversity in all three zones in the chained area compared with the intact remnant, and a number of abundant taxa restricted to particular zones. 4–5 years after disturbance some early colonisers were absent, but the plant assemblages were still distinct. The distribution and abundance of the Declared Rare species *Boronia adamsiana* occurring in the chained area was surveyed. The value of this managed disturbance within remnants in an agricultural landscape for rare and seral species is discussed.

Keywords: Succession, *Boronia adamsiana*, chaining, diversity, rare species, fire, vegetation mosaics

Introduction

Clearance of native habitat for agriculture is a global issue threatening native biodiversity (Tilman 1999). Land clearing in some areas of the wheat-growing region of Western Australia, commonly known as the wheatbelt, has resulted in losses of up to 97% of the native vegetation (Dilworth *et al.* 2000). The wheatbelt (including upper catchment areas) retains only 7% of its native vegetated area (Beecham 2004). A common method used to clear the land, referred to as 'chaining', was developed during the Second World War and involved the use of a chain or cable suspended between two tractors which was drawn along the ground (Beresford 2001). The cable rides over small trees tearing off limbs and leaving a medium for a fire which was then used to remove the bulk of the plant debris prior to cultivation. Similar techniques with a roller are used to create fire breaks and although they maintain species richness, can alter species composition compared to neighbouring unrolled habitat, with species capable of resprouting being advantaged and obligate post-fire reseeders, such as *Hakea* and *Allocasuarina* being disadvantaged with the absence of fire (Pelton & Conran 2002). Seed from serotinous species may not be released by rolling or chaining in the absence of fire (Gill 1976), but if they are, can be destroyed by subsequent fire (McCaw & Smith 1992).

The vegetation fragments within the wheatbelt are islands of native vegetation (mostly less than 400 ha in size) surrounded by agricultural land (Hobbs & Atkins 1988), and this fragmentation has had devastating consequences for the native flora and fauna (Hobbs & Huenneke 1992) and has contributed to population extinctions (Hobbs & Mooney 1998). The long-term sustainability of these fragments is dependent on both processes within the fragment, such as its size and disturbance history, and on its location within the broader landscape (Norton *et al.* 1995) which together affect the composition of the extant community.

Landscape fragmentation can alter disturbances occurring within native vegetation, including changes to fire regimes (Gill 1999; Carlquist 1974), typically the most common natural disturbance in the Western Australian landscape (Gill *et al.* 1981). The flora of small remnants are highly susceptible to increases in the frequency of fire, as death of adults and exhaustion of the seed bank can occur (Enright *et al.* 1996; Auld *et al.* 2000), with diminished chance of recolonisation from outside the remnant should they go locally extinct. Conversely the incidence of fire in many remnants has declined significantly with clearing due to the surrounding land use (Beecham 2002), and a common management practice is to protect remnants from disturbance by fire, and thus promote maintenance of a "climax" plant community.

Changes to disturbance regimes have important implications for species that require disturbance to regenerate. In addition, long-term removal of disturbance from a habitat may eliminate those species reliant on disturbance for regeneration unless they have a persistent seed bank. Early seral species often exhibit greater longevity in the seed bank than late seral species

(Chambers & MacMahon 1994), although survival rates are highly variable between species (Auld *et al.* 2000).

Fencing and protection of fragments alone is insufficient in many fragments to ensure biodiversity enhancement (Spooner *et al.* 2002). The incorporation of disturbance into the management of native fragments is an important consideration to promote biodiversity and prevent domination of sites by a few long-lived species (Maher 2007). Can alternate disturbances be introduced if fire events continue to be excluded from small remnants? A fortuitous event, the chaining and subsequent land abandonment of part of a small bushland remnant, has allowed the effects of a human induced disturbance to be studied. Our aims were to compare species assemblages between recently disturbed and 'climax' (remnant) habitats to determine the value of this type of anthropogenic disturbance for promoting plant succession and to determine if the type of disturbance facilitates the development of different successional trajectories.

Methods

Study Site

The 16.1 ha remnant is located about 2 km south of Westonia in the eastern central Wheatbelt (31°19'14"S, 118°41'37"E). The area has a Mediterranean climate with an average annual rainfall of about 300 mm (327 mm at Merredin about 55 km west of Westonia, 294 mm at Southern Cross about 60 km east of Westonia; Commonwealth Bureau of Meteorology 2007). Although surrounded by wheat fields, the remnant is about 600 m from the edge of the Westonia commons, consisting of about 5000 ha of remnant thicket and woodland vegetation (Fulton & Majer 2006). The remnant is not fenced and signs of domestic stock (sheep and cattle), feral herbivores (rabbits), and foxes were evident within the remnant.

Within the site are two major habitats; the remnant *Allocasuarina/Acacia/Eucalyptus burracoppineusis* thicket and a 6 ha area in the south east corner that was chained between April 2003 and April 2004 (Figure 1; Fulton & Majer 2006). The chained area was to be cleared and then converted into a wheat field, however, only some sections were cleared, some vegetation piles burnt and any further steps to convert it to a wheat field abandoned. These actions left three distinct disturbed zones within the chained area: Cleared – chained vegetation was cleared; Burnt – piles of cleared plants were burnt leaving areas with ash on the ground; Mulched – vegetation was chained and the debris left as it fell.

Sampling methods

During April and July 2006 the vegetation was sampled in 50 4x4 m quadrats. The size of the quadrats used in this study were relatively small, thereby creating greater heterogeneity within zones, but larger quadrats would have resulted in sampling across zones and reduced the ability to compare the zones within the chained area.

The location of each quadrat was determined by constructing eight north/south transects 50 m apart spanning the remnant and chained areas (Figure 1). Quadrats were positioned systematically along the
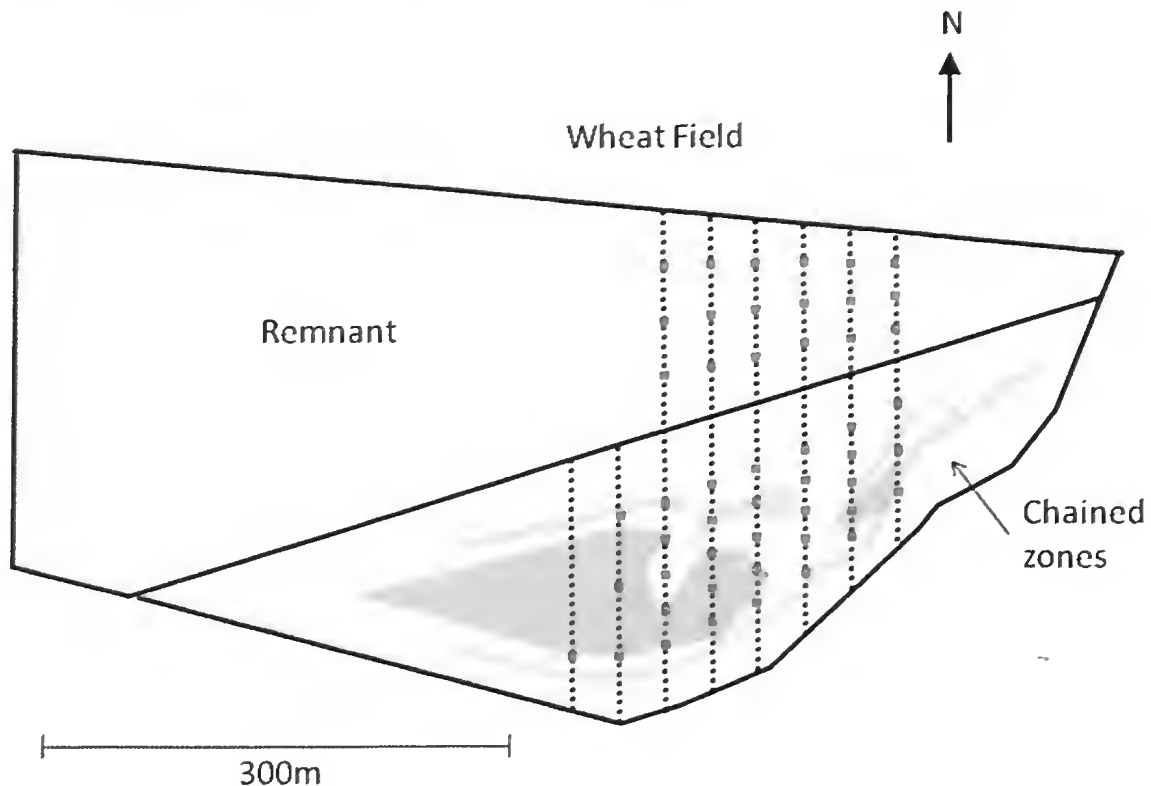

Figure 1. Sketch map of study site showing the extent of the chained zones. The approximate location of transects (dottled line) and sampling plots (squares) are indicated. Within the chained zones the approximate location of the mulched zone (dark central area) and areas where vegetation was burned (light shaded areas) is indicated with the remainder being cleared.

transect in the remnant and in the chained area and categorized by the type of disturbance in each quadrat (Undisturbed remnant, Cleared, Burnt, Mulched). For each species in a quadrat the total number of plants was counted and the percent cover estimated. For each quadrat the percent bare ground and litter cover was also estimated. In March 2008 a subset (20) of the quadrats were resurveyed. For all taxa a reference specimen was collected and where possible identified to species with the assistance of reference material at Curtin University and the Western Australian Herbarium. Due to the time of year of the study no annuals were recorded.

The distribution of *Boronia adamsiana* F.Muell (Barbalin boronia), a Declared Rare Flora (DRF) species found in the 2006 survey, was surveyed within the site in March 2008. All the chained area and 1.4 ha of the remnant were systematically searched. The height and width of each plant was measured and the presence/absence of seed set was recorded.

Data analysis

Repeated measures ANOVA was used to compare species richness between zones and years. One –way ANOVA was used to compare canopy height, ground cover percentages, and density of plants in each mode of regeneration between zones. Plant density data was log transformed prior to analysis. Post hoc LSD comparisons were performed where a significant ANOVA was obtained. The program SPSS (SPSS Inc. 2002) was used for these analyses. Two-sample t-tests assuming unequal variance were used to compare the height and crown diameter of *Boronia adamsiana* plants with and without seed.

Detrended correspondence analysis (DCA; Hill & Gauch 1980) was used to explore patterns of species association within the floristic data. DCA arranges quandrats along ordination axes, based on the taxon composition, and does not force association among groups. Relative to other ordination techniques, DCA has improved performance when data are heterogeneous (Hill & Gauch 1980). Cover data for each species was transformed to log $(x + 1)$ before ordination, which reduced the impact of very abundant species on the result. Blocked multi-response permutation procedure (MRPP; Mielke 1984) was used to test for differences between the quadrats from the 4 zones in 2006. For MRPP $A = 1 -$ (observed delta/expected delta). $A = 1$ when all items are identical within groups (delta = 0); $A = 0$ when heterogeneity within groups equals expectation

by chance; $A < 0$ when there is more heterogeneity within groups than expected by chance. P = probability of smaller or equal delta. The program PC-ORD (McCune & Mefford 1999) was used for these analyses.

Results

Vegetation patterns

A total of 94 vascular plant taxa were sampled from the 50 quadrats. The MRPP analysis indicated the *a-priori* groupings were distinct (MRBP; $A = 0.09$, $P < 0.001$). Ordination indicates general separation of the quadrats into three relatively distinct groupings (Figure 2). Quadrats from the burnt zone and the remnant were the most distinct with those from the other two zones intermediate. There was one major outlier from the remnant that plotted with the burnt quadrats. This quadrat was across an old fence line within the northern edge of the remnant and had minimal vegetation. An outlier from the chained and cleared zone stood alone on axis two in an initial ordination. It had 5 taxa (all less than 1% cover) unique to that plot and was located at the south eastern corner of the sampled quadrates. It was removed and the analysis rerun.

Species richness in 2006 differed significantly between habitats (MS = 135.9, d.f. = 3, p < 0.001) with the remnant having the lowest richness (5.9 taxa/quadrat). The chained and mulched zone (13.0 taxa/quadrat) had the highest species richness (Table 1).

Only *Baeckea elderiana*, *Drummondita hasselli* and *Allocasuarina* spp. had a high cover and/or abundance across all zones (Table 2). The canopy species *Allocasuarina* spp., *Acacia acuminata*, *Eucalyptus burracoppinensis* and the midstorey shrub *Baeckea elderiana* were the dominant cover in the remnant quadrats. In addition *Drummondita hasselli* and *Euryomyrtus maidenii* were abundant. Five taxa were recorded only in the remnant. Of the common taxa none was unique to the remnant, although *A. acuminata* was rare within the chained zones (Table 2). In general *Acacia* species were relatively abundant in the remnant, but rare within the chained area.

The chained and mulched zone had a high proportion of litter on the ground, and less bare ground than all other chained zones and similar to the remnant (Table 1). There was a high density of *Allocasuarina* seedlings resulting from the seeds shed from the cones of the chained vegetation. Equally abundant was the small

Table 1

Summary of canopy height, ground cover and taxon richness within each zone in 2006 (mean ± SE). For each parameter, zones with different letters are significantly different (LSD, p = < 0.05).

	Remnant	Chained & mulched	Chained & cleared	Chained & burnt
Quadrats	18	11	11	10
Canopy height	2.9 ± 0.2[a]	1.4 ± 0.2[b]	1.1 ± 0.2[b]	1.0 ± 0.2[b]
% bare ground	51.8 ± 7.1[a]	34.5 ± 3.9[a]	75.6 ± 5.0[b]	75.1 ± 3.7[b]
% litter cover	35.9 ± 7.5[a]	46.4 ± 4.4[a]	10.5 ± 2.1[b]	10.7 ± 2.5[b]
% vegetation cover	19.8 ± 5.3[a]	19.1 ± 3.2[a]	13.1 ± 2.8[a]	14.2 ± 2.0[a]
Species richness	5.9 ± 0.4[a]	13.0 ± 1.0[c]	9.5 ± 0.9[b]	11.2 ± 1.0[bc]
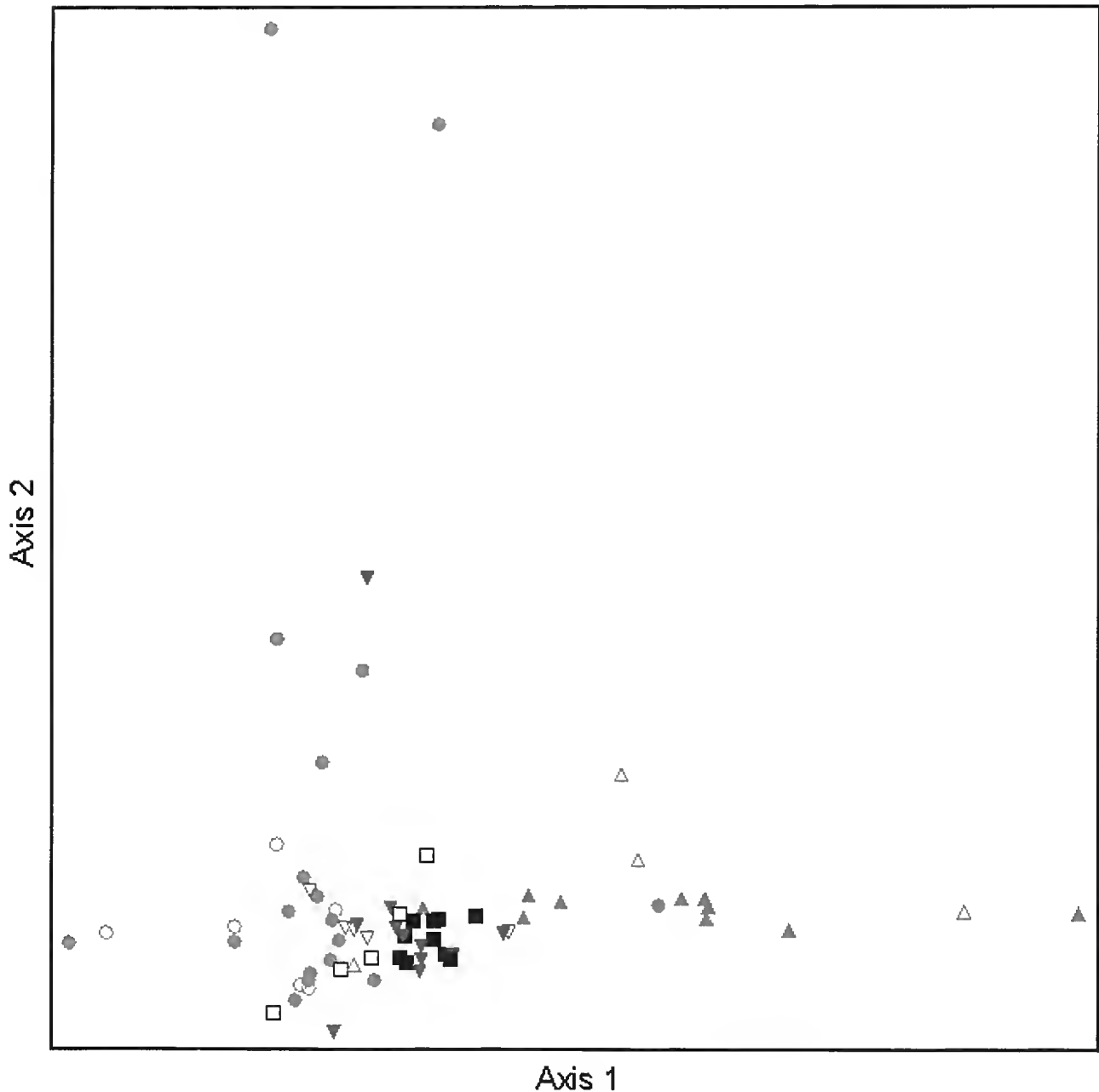
Figure 2. Ordination of vegetation cover in chained remnant across different zones. Zones: ● = remnant, ■ = chained & cleared, ▼ = chained & mulched ▲ = chained & burnt. Filled symbols are from 2006, open symbols from 2008. R^2 axis-1 = 0.15; R^2 axis-2 = 0.16. One chained and cleared plot which was an outlier on axis 2 was removed and the analysis rerun.

prickly shrub *Comesperma spinosum*, not sampled in the remnant and absent from quadrats in the burnt zone. Resprouting *Enryomyrtus maidenii*, *D. hassellii* and *E. burracoppinensis* were also abundant. 13 taxa were unique to the chained habitat and 33 other taxa not sampled in the remnant quadrats. Of the common taxa *E. maidenii* was predominant in this zone and a further 4 taxa present in this zone were not found in the remnant (Table 2).

In the chained and cleared zone *Gonocarpus confertifolius* var. *helmsii* was the most abundant taxon present and had the second highest cover after *Baeckea elderiana*. *Allocasuarina* spp. were also abundant. Thirteen taxa were unique to the cleared habitat and 26 of the species in the cleared zone were not found in the remnant quadrats. Of the common taxa *Grevillea paradoxa* was predominant in this zone and a further 4 taxa present were not sampled in the remnant.

In the chained and burnt zone *G. confertifolius* var. *helmsii*, *Kerandrenia integrifolia* and *Dampiera luteiflora* all from the soil seed bank were the most abundant taxa and had the greatest cover. 12 taxa were unique to the burnt habitat (but 8 of these were represented by a single specimen) and 33 species found in this zone did not occur in the remnant quadrats. Of the common taxa *K. integrifolia*, *D. luteiflora* and *Neurachne alopecuroidea* were predominant in this zone.

Those taxa identified to at least generic level were classified according to their mode of regeneration:

Table 2

Summary of important taxa (classified as having mean density > 2 plants per quadrat or average cover > 2% in any zone) within each zone from the 2006 survey of quadrats across a chained remnant. # indicates not found in quadrats sampled in 2008. Mode of regeneration: R = respouter; C = serotonous seeder; S = soil seedbank.

Family	Taxa	Mode of regeneration	Zone							
			Remnant		Chained & mulched		Chained & cleared		Chained & burnt	
			Density	Cover	Density	Cover	Density	Cover	Density	Cover
Casuarinaceae	*Allocasuarina corniculata & campestris*	C	2.6 ± 1.0	8.4 ± 2.9	12.1 ± 2.1	2.3 ± 0.3	6.8 ± 3.0	1.8 ± 0.6	1.0 ± 0.4	0.5 ± 0.2
Goodeniaceae	*Dampiera luteiflora*	S	0	0	0.5 ± 0.4	0.2 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	6.6 ± 4.0	1.2 ± 0.5
Haloragaceae	*Gonocarpus confertifolius* var. *helmsii* #	S	0	0	0.4 ± 0.2	0.2 ± 0.1	14.4 ± 5.9	1.9 ± 0.9	9.0 ± 2.7	2.3 ± 0.9
Mimosaceae	*Acacia acuminata*	S	0.5 ± 0.3	6.1 ± 4.4	0	0	0.1 ± 0.1	0.0 ± 0.0	0	0
	Acacia sp.	S	0.5 ± 0.2	2.4 ± 1.3	0	0	0	0	0.7 ± 0.7	0.5 ± 0.5
Myrtaceae	*Baeckea* sp.	R	0.2 ± 0.2	0.3 ± 0.3	3.8 ± 1.5	0.9 ± 0.2	0	0	0	0
	Baeckea ?*behrii*	R	2.7 ± 1.3	1.6 ± 1.0	1.0 ± 1.0	0.4 ± 0.4	0	0	0	0
	Baeckea elderiana	R	16.3 ± 5.3	8.1 ± 2.9	3.7 ± 1.9	1.0 ± 0.3	4.7 ± 1.5	2.5 ± 0.9	2.1 ± 1.3	1.1 ± 0.7
	Eucalyptus burracoppinensis	R	1.2 ± 0.5	3.6 ± 2.8	0.9 ± 0.4	3.2 ± 2.8	0.9 ± 0.3	0.7 ± 0.3	1.2 ± 0.5	0.5 ± 0.2
	Euryomyrtus maidenii	R	4.1 ± 1.7	0.8 ± 0.3	8.3 ± 2.5	1.2 ± 0.4	0.3 ± 0.3	0.1 ± 0.1	1.3 ± 0.7	0.4 ± 0.2
	Melaleuca conothamnoides	R	0.8 ± 0.4	0.4 ± 0.2	3.4 ± 1.3	1.7 ± 0.9	0.5 ± 0.3	0.4 ± 0.2	0.8 ± 0.6	0.5 ± 0.3
Poaceae	*Amphipogon* sp.	R	1.5 ± 0.7	0.2 ± 0.1	2.4 ± 1.9	0.9 ± 0.4	0.3 ± 0.1	0.2 ± 0.1	0	0
	Neurachne alopecuroidea	R	0	0	1.3 ± 0.7	2.9 ± 1.3	0.5 ± 0.4	1.1 ± 0.9	5.3 ± 5.0	0.6 ± 0.2
Polygalaceae	*Comesperma spinosum*	R	0	0	16.2 ± 4.8	2.8 ± 0.9	1.5 ± 1.2	0.4 ± 0.3	0	0
Proteaceae	*Grevillea paradoxa*	S	0.4 ± 0.4	0.0 ± 0.0	0	0	2.9 ± 2.1	0.2 ± 0.1	0	0
Rutaceae	*Drummondita hasselii*	R	4.4 ± 1.9	1.0 ± 0.3	8.6 ± 2.4	2.3 ± 0.9	3.7 ± 2.4	0.3 ± 0.1	1.8 ± 0.5	0.8 ± 0.1
Sterculiaceae	*Keraudrenia integrifolia*	S	0.2 ± 0.1	0.3 ± 0.2	0.2 ± 0.2	0.0 ± 0.0	0.6 ± 0.2	0.2 ± 0.1	8.2 ± 2.5	2.3 ± 0.5

resprouter, serotinous seeder, and from the soil seed bank (Appendix 1). Serotinous seeder density varied significantly among zones with the burnt zone having the lowest density compared with their density in the other zones (MS = 1.999, d.f. = 2, p < 0.001; Figure 3). Resprouter density differed between zone with the cleared area having the highest density (MS = 1.952, d.f. = 2, p < 0.001; Figure 3). The density of species from the seed bank also differed between zone with the mulched zone having the lowest density (MS = 1.498, d.f. = 2, p < 0.001; Figure 3).

Changes between 2006 and 2008

There was significant variation in species richness among zones and this effect was consistent between years (Figure 3; MS = 144.9, d.f. = 1, p < 0.001 (year); MS = 64.4, d.f. = 3, p = 0.012 (zone) and MS = 3.69, d.f. = 3, p = 0.58 (time × zone). The remnant and the chained and cleared zone had the lowest species richness, the chained and mulched the highest, and the chained and burnt zone had species richness that was intermediate between these two extremes (Figure 4). Notable changes in species composition between the two sampling periods were the disappearance of *Gonocarpus confertifolius* var *helmsii* which was very abundant in 2006, an increase from very low levels in the abundance of 3 *Acacia* species in the chained zones, and an increasing cover of *Allocasuarina* spp. and *Eucalyptus burracoppinensis*. Generally quadrats still fell within the same grouping as 2006 although they were generally closer to the remnant quadrats in 2008 than in 2006 (Figure 2).

Boronia survey

Eighty seven *B. adamsiana* individuals were located in the chained region, while none was found in the 1.4 ha of remnant searched. Plants of this species were recorded in all 3 chained zones in the quadrat survey in low densities (0.1, 0.5, and 0.1 plants per quadrat for the burnt, cleared, and mulched zones respectively). Only 5 of the 88 plants found across the site were in a burnt zone, the rest spread equally between the chained and mulched zones. About 36% of the plants had evidence of having produced seed and these were significantly taller (t = 3.5, d.f. = 82, p < 0.001) and had a larger mean crown diameter (t = 6.4, d.f. = 75, p < 0.001) than underproductive plants (Table 3; Figure 5).

Discussion

Disturbance of this remnant through chaining has had a beneficial response in terms of above ground plant species richness. It has allowed numerous species to establish in the disturbed area. The fortuitous creation of different zones within the chained areas due to the incomplete land conversion has likely promoted different species within each zone.

Diversity and disturbance

Fragmentation of vegetation communities alters disturbance regimes within them (Saunders *et al.* 1991). Maintaining such remnants in a climax state through a "lock and key" approach, through attempting to remove disturbances such as fire from the landscape can lead to a dominance of relatively few canopy and midstorey shrubs, and a relatively sparse ground cover (Maher 2007). Some areas within the remnant zone are very species poor with mature vegetation senescing, and no evidence of replacement. Continued maintenance of remnants in this state may eventually simplify the
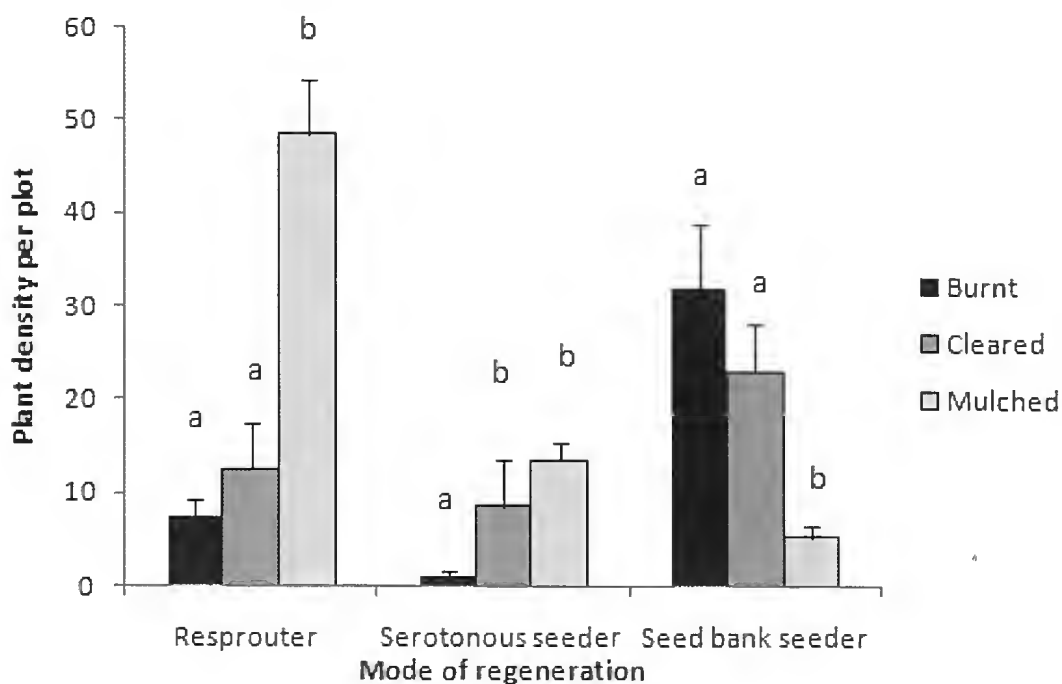
Figure 3. Density of resprouters and seeders (serotinous and seed bank storage) within each of the zones within the chained area. Data are means ± SE. Within each mode of regeneration zones with different letters have significantly different densities (LSD, p = < 0.05).
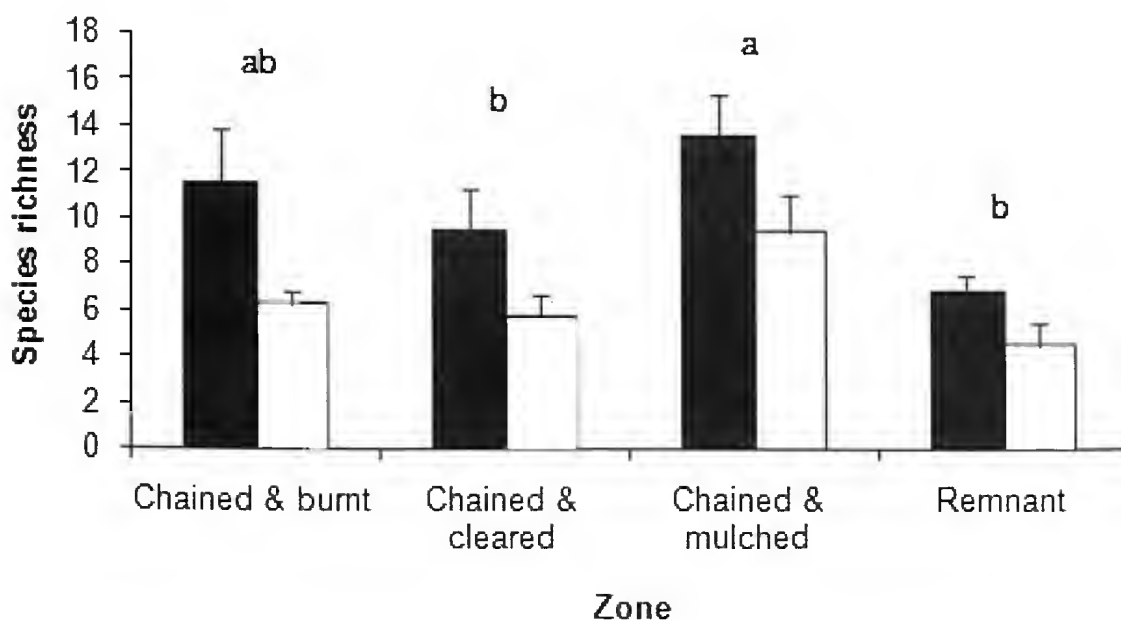
Figure 4. Species richness sampled within quadrats in each zone in 2006 (black) and 2008 (white). Zones with different letters have significantly different species richness (LSD, p = < 0.05).
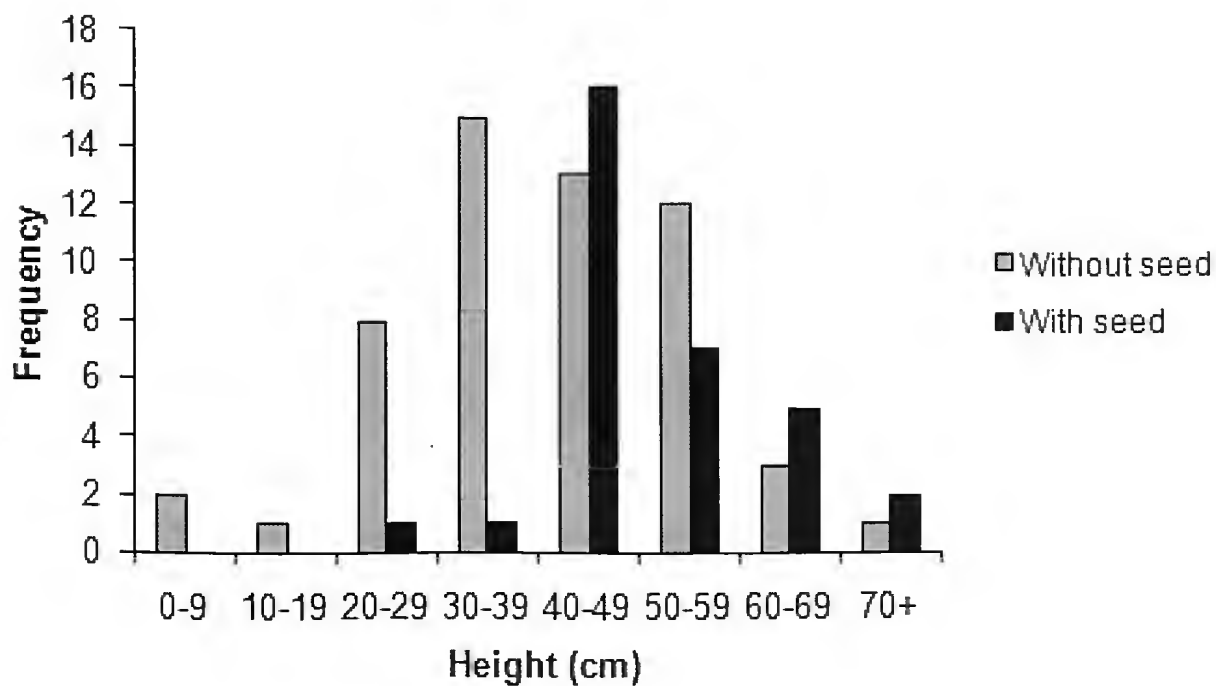
Figure 5. Size distribution of *Boronia* plants with and without evidence of seeding.

Table 3

Size (mean +/- SE (range)) and reproductive status of *Boronia adamsiana* occurring in chained vegetation.

	With Seed	Without Seed	Total
Height (cm)	49.5 +/- 1.9 (22–72)	40.2+/- 2 (8.9–95)	43.9 +/- 1.5 (8.9–95)
Crown Diameter (cm)	34.6 +/- 1.5 (16–53)	27.3 +/- 1.4 (5–56.5)	30.2+/- 1.1 (5–56.5)
n	32	55	87

community, even if there is subsequent disturbance, if the length of time between disturbances exceeds the seed bank life span (Whelan 1995; Bond & van Wilgen 1996). Furthermore there are limited dispersal opportunities for many of the seral species across the surrounding agricultural landscape if they are no longer represented in the seed bank.

Clearly many species have survived in the seedbank in this remnant despite what is probably a long period since disturbance by fire. Persistence in the seed back is unknown for many native species. It is likely to be highly variable between taxa (e.g., Weston 1985; Auld et al. 2000; Ooi et al. 2007), appears at best weakly related to seed size (Leishman & Westoby 1998; Moles & Westoby 2004), and varies with different temperature and rainfall conditions and burial depths (Owens et al. 1995; Hill & Vandeer Kloet 2005).

Disturbance caused by the chaining and associated clearing and fire, clearly promotes above ground diversity within this forest remnant from the soil seed bank, as has been shown elsewhere (Denslow 1980; but see Hubbell et al. 1999). However, there may have been an overestimate of the increase in diversity as some of the rarer specimens in quadrats were very small and so difficult to identify and may be represented as mature plants in other quadrats. Presumably if further disturbance involved in conversion of the land for agriculture proceeded, this promotion of above ground diversity would be lost. Many of the canopy species have a relative short seed bank life span and rely on regular seed production (Auld 1995) and therefore would not likely re-establish if there was a prolonged period of disturbance before the site was left to recover.

It appears likely that the different zones have different successional pathways and will lead to different species compositions in the climax assemblage. Areas that are chained and then burnt will likely have an under-representation of serotinous seeders in the canopy (in this case *Allocasuarina* and *Hakea*) compared to the other zones, and a greater representation of soil seed bank species such as *Acacia* that are dependant of fire for germination. A short period between chaining and burning, before seed is released from pods may minimise losses of serotinous taxa from the burnt zone (McCaw & Smith 1992). Resprouters appear in greatest abundance in the mulched zone and least abundance in the burnt, which may be due to the increased protection offered by the mulch and/or minimal disturbance compared to the burning and clearing that occurred post chaining in the other zones. The increased competition from resprouters and serotinous seeders may account for the reduced density of soil seed bank taxa in the mulched zone relative to the other zones.

Some of the observed differences in plant taxa between zones could be explained by pre-existing spatial differences in extant taxa and differences in the seral species in the soil seed bank prior to chaining. The vegetation was not surveyed prior to disturbance, and changes in vegetation over small spatial scales are common in WA (e.g., Craig et al. 2008). However there was no obvious differences in the sandy soil across the chained area, nor between the southern margin of the remnant and the chained area (the northern margin of the remnant is slightly stonier). However, this seems unlikely to explain all the difference as the burnt zone is a relatively narrow strip that runs across the site in close proximity to both the other zones, and patterns of presence or absence of some taxa can be explained by known response to presence or absence of fire.

Somewhat surprising was the relatively low abundance of weed species in the chained area, 3 taxa all in low abundance, despite the small size of the remnant and the surrounding fellow wheat fields containing various weed species. This indicates the site has a relatively high resistance to weed invasion, and that the chaining has not significantly reduced this resistance. This may reflect the limited grazing disturbance that this predominantly cropping landscape has had compared to other areas of the wheatbelt, and the possible resilience of parts of this ancient landscape to fragmentation (Yates & Hobbs 1997; Hobbs 2001; Hopper 2009 but see Standish & Hobbs 2009).

The lower diversity of species in all zones in 2008 probably reflects differences in the search efficiency of the surveyors for the rare taxa, as the remnant site is unlikely to have changed significantly over 2 years. However, there were clear changes in some dominant species within the communities in the chained zones consistent with vegetation succession; seral species becoming less abundant and species dominant in the remnant area increasing in density and cover within the chained zones.

Value of chaining and maintaining a mosaic of habitats in remnant management

Although fire is a common form of disturbance and promoter of diversity in the Australian landscape (Penman et al. 2008) only a small proportion of the species colonising the chained area were largely restricted to the burnt zone and appeared to require direct contact with fire. Physical disturbance caused by the chaining appeared adequate for many species, such as the DRF *B. adamsiana* to establish within the chained area and greatly increased the overall diversity of species growing within this remnant. Therefore chaining could be a useful management tool to promote diversity and maintenance of seral species in areas where fire is unwanted or needs to be limited so as not to affect an entire remnant or adjacent infrastructure. The chained vegetation does not necessarily need to be cleared, although its remaining *in situ* would increase the fuel load and subsequent risk of fire. Chaining with subsequent fire would alter community structure compared to a fire alone, with serotonous seeders particularly venerable (McCaw & Smith 1992; Pelton & Conran 2002; Gosper et al. 2010). Plants that rely on fire for recruitment (many *Acacia* for example) may also have fewer opportunities for regeneration if fires were eliminated altogether (Buist et al. 2002).

Although not directly affected by fire, some of the species may have been stimulated to germinate from the soil seed bank by the smoke or heat generated from the nearby burnt vegetation piles as has been demonstrated in the laboratory (Dixon et al. 1995; Enright et al. 1997; Baker et al. 2005). If this is the case then incorporation of fire into parts of the chained area would be needed to aid persistence of more species than just those we recorded unique to the burnt zone.

Disturbance does promote above ground diversity, but promoting chaining at a site should only be necessary if other disturbances are so infrequent that the soil-stored seedbank has become diminished, which may take decades or even centuries for some taxa (Weston 1985), so its application would need to be carefully considered. The use of chaining will also result in a different successional trajectory compared to burning (Gosper *et al*. in press).

Rare species

The population of the DRF *Boronia adamsiana* is outside its previously recorded range, with the nearest record about 70 km NW of this site (Mollemans *et al*. 1993; Davis 2005). This is not altogether unexpected as other plants thought to be extinct or rare have had significant range extensions recorded from sites surveyed after fire (Yates *et al*. 2003). It is also suspected to have occurred in an area revegetated after quarrying on the edge of Sandford Rock Nature Reserve, about 13 km NE of this study site (PM pers. obs.), although brief searches for specimens in 2008 did not locate any remaining plants.

Boronia adamsiana was once thought to be extinct (Hopper *et al*. 1990), but is now known from a number of populations (Mollemans *et al*. 1993; Davis 2005) including those on roadsides (Beecham 2002). Of the nine populations reported by Mollemans *et al*. (1993) four were on private properties within areas cleared with chains and left to regenerate. In 1993, three populations had senescing plants and appeared to be in decline (Mollemans *et al*. 1993). It is likely that ongoing disturbance would be required to maintain a population of this species at a site as it occurs in early succession stages after disturbance. However, seed of this species is clearly persistent in the seed bank, with no source populations nearby, an absence of plants within the unchained remnant, and the suspected absence of fire within this remnant for many years.

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Appendix 1

List of taxa identified to at least generic level and likely mode of regeneration. * denotes introduced species.

Family	Taxa	Mode of regeneration
Asteraceae	*Conyza* sp.*	Soil seed bank
Aizoaceae	*Mesembryanthemum crystallinum**	Soil seed bank
Boryaceae	*Borya* sp.	Soil seed bank
Casuarinaceae	*Allocasuarina corniculata* & *campestris*	Canopy stored seed
Celastraceae	*Stackhousia monogyna*	Soil seed bank
Cucurbitaceae	*Cucumis myriocarpus**	Soil seed bank
Cyperaceae	*Lepidosperma gracile*	Resprouter
Dilleniaceae	*Hibbertia ?racemosa*	Soil seed bank
Euphorbiaceae	*Beyeria* sp.	Soil seed bank
Goodeniaceae	*Dampiera luteiflora*	Soil seed bank
	Dampiera stenostachya	Soil seed bank
	Dampiera wellsiana	Soil seed bank
	Goodenia pinifolia	Soil seed bank
	Velleia connata	Soil seed bank
	Verreauxia villosa	Soil seed bank
Gyrostemonaceae	*Gyrostemon racemiger*	Soil seed bank
	Gyrostemon sp.	Soil seed bank
Haloragaceae	*Glischrocaryon* spp.	Soil seed bank
	Gonocarpus confertifolius var *helmsii*	Soil seed bank
Lamiaceae	*Cyanostegia microphylla*	Soil seed bank
	Cyanostegia sp.	Soil seed bank
	Pityrodia lepidota	Soil seed bank
	Pityrodia terminalis	Soil seed bank
Mimosaceae	*Acacia acuminata*	Soil seed bank
	Acacia sp.	Soil seed bank
	Acacia longispinea	Soil seed bank
	Acacia ?neurophylla	Soil seed bank
Myrtaceae	*Baeckea* sp.	Resprouter
	Baeckea ?behrii	Resprouter
	Baeckea elderiana	Resprouter
	Calothamnus longissimus	Resprouter
	Chamelaucium sp.	Soil seed bank
	Eucalyptus burracoppinensis	Resprouter
	Eucalyptus leptopoda	Resprouter
	Euryomyrtus maideni	Resprouter
	Melaleuca conothamnoides	Resprouter
	Micromyrtus sp.	Resprouter
	Regelia sp.	Resprouter
Myoporaceae	*Eremophila* sp.	Soil seed bank
Papilionaceae	*Daviesia nematophylla*	Soil seed bank
	Mirbelia rhagodioides	Soil seed bank
Poaceae	*Amphipogon* sp.	Resprouter
	Neurachne alopecuroidea	Resprouter
Polygalaceae	*Comesperma spinosum*	Resprouter
Proteaceae	*Grevillea eriostachya*	Soil seed bank
	Grevillea hookeriana subsp. *apiciloba*	Soil seed bank
	Grevillea paradoxa	Soil seed bank
	Hakea francisiana	Canopy stored seed
Rutaceae	*Boronia adamsiana*	Soil seed bank
	Drummondita hassellii	Resprouter
	Phebalium tuberculosum	Soil seed bank
	Philotheca tomentella	Soil seed bank
Santalaceae	*Exocarpos aphyllus*	Soil seed bank
	Leptomeria sp.	Soil seed bank
Sterculiaceae	*Kerandrenia integrifolia*	Soil seed bank
Stylidiaceae	*Stylidium* sp.	Soil seed bank
Thymelaeaceae	*Pimelea aeruginosa*	Soil seed bank
	Pimelea angustifolia	Soil seed bank
Xanthorrhoeaceae	*Xanthorrhoea* sp.	Resprouter

Black-stripe minnow *Galaxiella nigrostriata* (Shipway 1953) (Pisces: Galaxiidae), a review and discussion

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Abstract

Galaxiella nigrostriata is a small freshwater fish endemic to the southwest of Western Australia. *Galaxiella nigrostriata* are unusual because they aestivate in the sediments of seasonal wetlands when the wetlands dry over summer. Although once thought to be more extensively distributed in coastal wetlands between Moore River and Albany, they are now only found in three remnant populations on the Swan Coastal Plain and wetlands between Augusta and Albany. This review brings together all aspects of *G. nigrostriata's* life cycle, the most significant findings of research to date and highlights areas lacking in knowledge, most importantly aestivation habits. With the main threats to their conservation being a drying climate, increasing pressure on groundwater resources and competition for land use, research is needed to direct management of this charismatic species, particularly within remnant populations.

Keywords: Black-stripe minnow, *Galaxiella nigrostriata*, Galaxiidae, seasonal wetlands, aestivate, Swan Coastal Plain, south-west Western Australia

Introduction

The Galaxiidae family are freshwater fish thought to have Gondwanan origins and are found below 32° south within cool-temperate regions in the southern hemisphere, namely, South America, southern Africa, New Caledonia, New Zealand and Australia (McDowall & Frankenberg 1981; Allen *et al.* 2002; McDowall 2006). The Galaxiidae consist of 8 genera and *ca.* 56 species, of which 4 genera and 20 species are found in Australia (McDowall 2006). There are only three species in the galaxiid genus *Galaxiella*, and are all located in southern Australia (Allen *et al.* 2002). *Galaxiella nigrostriata* and *G. munda* (mud minnow) inhabit the south-west of WA, and *G. pusilla* (dwarf galaxiid) is found from south-eastern South Australia to southern Victoria and northern Tasmania (Morgan *et al.* 1998; Allen *et al.* 2002). The south-west region of Western Australia (WA) has ten native freshwater fish species, of which eight are endemic (Morgan *et al.* 1998). Of the endemic species three are Galaxiidae, including *Galaxiella nigrostriata* (Morgan *et al.* 1998).

Galaxiella nigrostriata is a small endemic freshwater fish that lives in seasonal wetlands in south-west Western Australia, spread between Augusta and Albany and in three remnant populations on the Swan Coastal Plain (SCP) (Morgan *et al.* 1998; Smith *et al.* 2002b; McLure & Horwitz 2009). The three populations on the SCP are believed to be naturally occurring remnants of a greater distribution on the SCP (Morgan *et al.* 1998; Smith *et al.* 2002b), prior to widespread habitat destruction that

followed European colonisation over the last 180 years (Hill *et al.* 1996; Horwitz *et al.* 2009). It is thought that up to 80% of wetlands on the SCP in WA have been drained or otherwise degraded, mostly for urbanisation and agriculture (Seddon 1972; Balla 1994; Davis & Froend 1999). This figure is likely to increase with ongoing urban and rural expansion and predicted ongoing declining rainfall patterns across south-west WA (Watterson *et al.* 2007) continuing to reduce the fisheries value and size, and number of remaining wetlands in this area. Indeed, the reduced distribution of many native freshwater fish species to the relatively pristine areas of the south-west corner of WA is considered to be due to widespread degradation of wetlands on the SCP (Morgan *et al.* 1998; Allen *et al.* 2002). Unfortunately, the sanctuary of national parks where many of the southern *G. nigrostriata* populations remain may also be subject to external pressures (Trayler *et al.* 1996). These conservation issues are not restricted to south-west WA, wetlands in other temperate regions (Brinson & Malvárez 2002; van Diggelen *et al.* 2006), groundwater influenced wetlands (Danielopol *et al.* 2003; Martínez-Santos *et al.* 2008) and wetlands in general throughout Australia and around the world are facing the same ongoing problems (Semlitsch & Bodie 1998; Finlayson & Rea 1999; Baron *et al.* 2002).

This review was undertaken to facilitate further research and management of *G. nigrostriata*. Given their preference for seasonal wetlands and the issues associated with that type of habitat, their future faces many challenges. We intend that the information provided here will give a good starting point for land managers to begin their conservation efforts for this charismatic endemic species.

Figure 1. Adult *Galaxiella nigrostriata*, approximately 30 mm total length. (Courtesy G. Allen)

Description

Galaxiidae are scaleless fish that have only one dorsal fin, typically have slender cylindrical bodies and maximum lengths range from 40 mm (*G. pusilla*) to 580 mm (*Galaxias argenteus* – New Zealand) (McDowall 1990; Allen *et al.* 2002; McDowall 2006). *Galaxiella*, along with the small monospecific genus *Brachygalaxias* is distinct within the *ca.* 56 species of Galaxiidae for having, among other differences, a lateral longitudinal orange stripe, less than seven pelvic fin rays, a large eye relative to their head size (28–30% of head length) and a fleshy abdominal keel (McDowall & Waters 2004).

Galaxiella nigrostriata are small galaxiid fish (Figure 1), maximum total length (TL) is about 48 mm, with an elongate body that is mostly grey-tan with a white ventral surface (Morgan *et al.* 1998; Allen *et al.* 2002). From early larval stages *G. nigrostriata* has dark pigmentation on the dorsal surface from snout to tail and ventrally from the dorsal surface of the gut to tail, with yellow to red pigmentation between (Gill & Neira 1994; McDowall & Waters 2004). The pigmentation becomes more concentrated as the fish mature, turning into two prominent black stripes surrounding a bright yellow to red stripe running laterally between the eye and tail (Morgan *et al.* 1998). The stripes become especially vivid while spawning, between June and September, then fade soon after (Morgan *et al.* 1998; Allen *et al.* 2002). *Galaxiella nigrostriata* become sexually mature when nearly one year old and die soon after spawning (Pen *et al.* 1993), although they have been known to live up to two years in aquaria (M. Bamford, Bamford Consulting Ecologists, 2008, pers. comm.)

Distribution

Southern populations of *G. nigrostriata* are located between Augusta and Albany, with the majority found on the Scott Coastal Plain, centred near Northcliffe in the D'Entrecasteaux National Park (Figure 2) (Morgan *et al.* 1998; Morgan & Gill 2000). There are three known remnant populations: a population discovered in 2009 at Lake Chandala *ca.* 50 km N of Perth (near Muchea), *ca.* 30 km NNE of Perth at wetland EPP173 in Melaleuca Park and 130 km south of Perth in wetlands within the

Kemerton Nature Reserve near Bunbury (Morgan *et al.* 1998; Bamford & Bamford 2002; Knott *et al.* 2002; McLure & Horwitz 2009). There was an ambiguous record from 1972 in the Carbunup River, south of Busselton, listed as *Brachygalaxias pusillus* and striped galaxias (Griffiths 1972). It was assumed to be *G. nigrostriata* (Morgan *et al.* 2004), probably due to the names used (see Taxonomy and Nomenclature) and the similarity shown in line drawings of the fish in the report. However, there have been no other records of *G. nigrostriata* in that area and the habitat is more suited to *G. munda*, which are known from there, so the fish may have been misidentified.

The remnant locations are *ca.* 380, 360 and 210 km north of the southern population. The discovery of the Lake Chandala population extends their known distribution further north and suggests other unknown populations may still exist. Coincidently, papers by Morgan *et al.* (1996, 1998) suggested *G. nigrostriata* had been found near Gingin, *ca.* 80 km north of Perth and *ca.* 30 km north of the recently discovered Lake Chandala population. Unfortunately, as foresighted as it was, that information was entered incorrectly; Morgan *et al.* were referring to records of *G. munda* near Gingin (D. Morgan, Centre for Fish and Fisheries Research, Murdoch University, 2009, pers. comm.).

Galaxiella nigrostriata distribution appears to have been incorrectly listed in some publications over the last 30 years as extending east to Esperance. This incorrect distribution is based on Western Australian Museum (WAM) records, from which an entry error for a holotype specimen was listed as collected from Marbelup Creek near Esperance (WAM, 2008, unpublished data). The entry should have been Marbelup Brook, *ca.* 20 km NW of Albany, which is among the eastern-most record. This error has now been rectified in the museum records (S. Morrison, WAM, 2009, pers. comm.).

Habitat

Galaxiella nigrostriata typically inhabit highly tannin stained water *ca.* 300 mm deep, with a pH and temperature range of 3.0–8.0 and 11–30°C respectively (Jaensch 1992; Gill & Morgan 1996; Morgan *et al.* 1998; Allen *et al.* 2002). *Galaxiella nigrostriata* larvae are thought
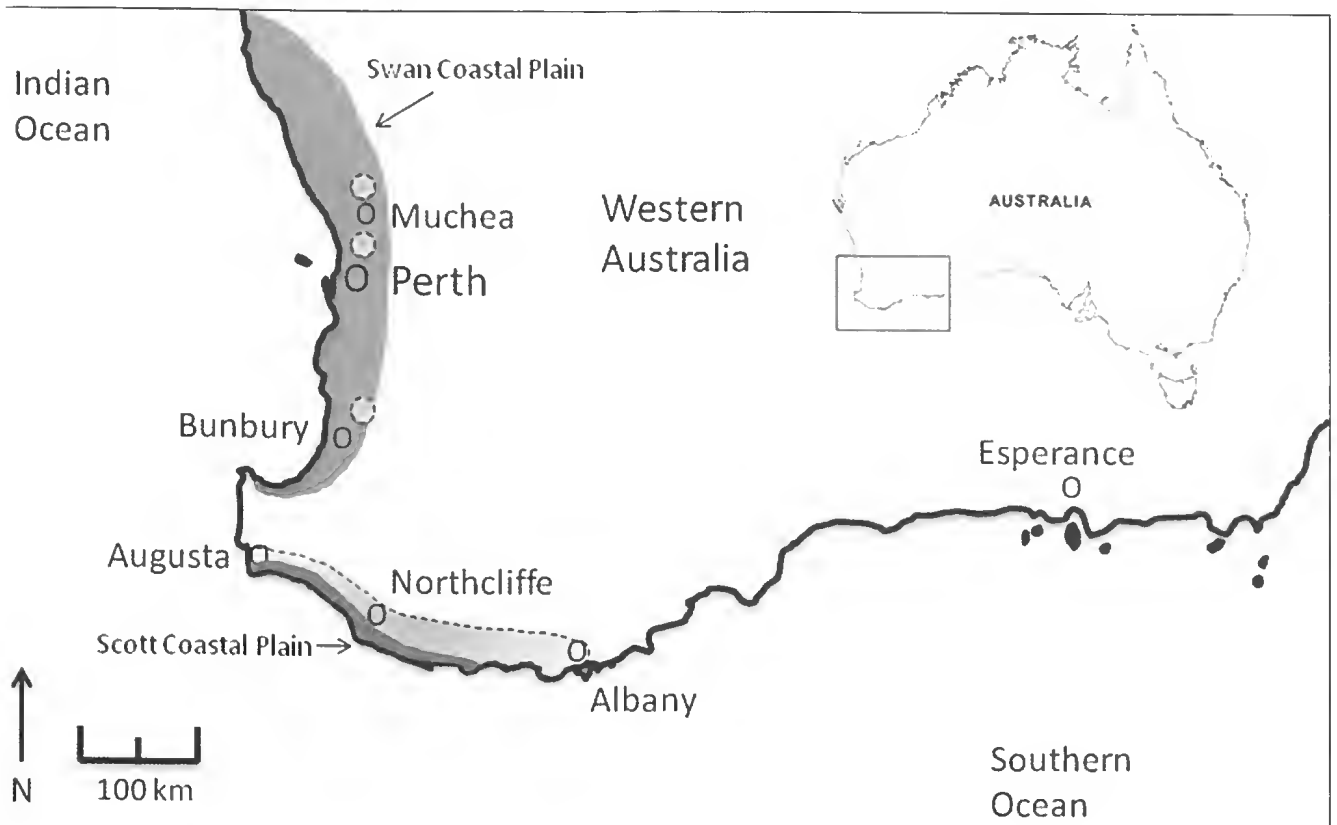
Figure 2. Present population areas of the *G. nigrostriata* in south-west Western Australia shown as light shaded areas. Dark shading shows location of Swan and Scott Coastal Plains.

to prefer open water and as they mature are more likely to be found in areas of macrophytic or riparian vegetation (Morgan *et al*. 1998; D. Galeotti 2008, unpublished data). *Galaxiella nigrostriata* have been recorded in slow-moving streams and lakes (McDowall & Frankenberg 1981; Jaensch 1992; Morgan *et al*. 1998), but are typically found in seasonal wetlands up to 100 km from the coast, with limited connectivity to nearby wetlands or rivers (Pusey & Edward 1990; Morgan & Gill 2000). *Galaxiella nigrostriata* are often found co-habiting with *Lepidogalaxias salamandroides* (salamanderfish), due to similarities in their preferred habitat, *i.e.*, their ability to tolerate seasonal wetlands by aestivating (Jaensch 1992; Morgan & Gill 2000; McDowall 2006).

Wetlands that *G. nigrostriata* inhabit are generally surrounded by fringing and riparian vegetation such as paperbarks (*Melaleuca* sp.) and rushes (*Baumea* sp.) (Morgan *et al*. 1998; Knott *et al*. 2002). These wetlands can be found within karri and jarrah forest (*Eucalyptus diversicolor* and *E. marginata*) and coastal peat flats in the south of WA, and *Banksia menziesii* open woodlands where the northern remnant populations exist (Morgan *et al*. 1998; Knott *et al*. 2002). *Galaxiella nigrostriata* have not been found in wetlands surrounded by cleared farmland (Morgan *et al*. 1998), which may underscore an important role of riparian vegetation as has also been found with other members of the Galaxiidae (Hicks & Barrier 1996; Bonnett & Sykes 2002) and other fish species (King & Warburton 2007). Wetlands within the southern

population's main area of distribution generally dry completely around December and remain dry until winter rains begin around June (Pusey & Edward 1990).

Diet

Pusey & Bradshaw (1996) suggested *G. nigrostriata* are primarily carnivorous and feed in the upper water column and the surface, with their diet following seasonally available prey. Other research showed populations of juveniles and adults (>20 mm TL) recorded near Northcliffe consumed zooplankton, flying ants and adult dipteran (flies) throughout the year, and in summer and autumn dipteran pupae and larvae and diatoms were also taken (however, the benthic algae is likely to be incidental ingestion) (Pen *et al*. 1993; Gill & Morgan 1996; Smith *et al*. 2002b). In winter, preflexion to flexion *G. nigrostriata* larvae (7–11 mm TL) predominantly fed on zooplankton, and postflexion larvae (12–23 mm TL) ate Collembola (springtails) and dipteran larvae (Gill & Morgan 2003). The diet of the northern Perth population at Melaleuca Park was very similar to the southern population, except for lower quantities of terrestrial insects being eaten (5% of total intake at Melaleuca Park compared to 20–50% near Northcliffe) (Smith *et al*. 2002b). These diet studies suggest *G. nigrostriata* are opportunist water column feeders with some surface feeding occurring as well, similar to other congenerics (Pusey & Bradshaw 1996; Smith *et al*. 2002b; Gill & Morgan 2003) *Galaxiella*

nigrostriata do not seem to compete for food with their main co-inhabitant, *L. salamandroides*, in the southern populations as *L. salamandroides* are primarily benthic feeders (Pusey & Bradshaw 1996; Gill & Morgan 2003).

Reproduction

Reproductive behaviour of *G. nigrostriata* is not fully understood, however parallels may reasonably be drawn with the congeneric *G. munda* and *G. pusilla* (McDowall & Waters 2004). It is thought that the fleshy abdominal keel is used to guide the female onto surfaces such as leaves or rocks to precisely lay her individual eggs (McDowall & Waters 2004), which are then fertilised by the male, as observed in the *G. pusilla* (Backhouse 1983). Each female *G. nigrostriata* lays *ca.* 60 eggs per season, possibly over a period of a couple of weeks (Pen *et al.* 1993). When the larvae hatch they are about 3.5 mm TL and both males and females develop their stripes soon after (Gill & Neira 1994; Morgan *et al.* 1998).

Spawning in the southern populations of *G. nigrostriata* occur between June and September, from mid-winter to mid-spring (Gill & Neira 1994; Morgan *et al.* 1998). Spawning peaks during mid-winter when water temperatures and daylight hours are at a minimum (Pen *et al.* 1993; Gill & Neira 1994; Morgan *et al.* 1998). *Galaxiella nigrostriata* at Melaleuca Park are reported to begin spawning a month later than the southern populations, and the Kemerton population may start around August (Smith *et al.* 2002b; Bamford & Bamford 2003).

Aestivation

Galaxiella nigrostriata aestivation was explored by Smith *et al.* (2002b) at Melaleuca Park while the wetland was dry, by fencing two drains entering the wetland (using fine mesh). Adult *G. nigrostriata* were present after the wetland had refilled in winter, having survived summer in the dry wetland. Other researchers have artificially flooded small dry wetland pools and found adult *G. nigrostriata* emerging within hours (Berra & Allen 1989b; Morgan *et al.* 1996). *Galaxiella nigrostriata* have also been found in isolated seasonal wetlands which may go years without connecting to neighbouring wetlands (D. Galeotti 2009, unpublished data). Within Galaxiidae, aestivation is limited to *G. nigrostriata* and *L. salamandroides* (south-west WA), possibly *G. munda* (south-west WA) and *G. pusilla* (south-eastern Australia and northern Tasmania), six *Neochanna* spp. (mudfish, in New Zealand, Tasmania and southern Victoria) and *Brachygalaxias bullocki* (red jollytail, in Chile) (McDowall 2006).

Anecdotal observations have suggested *G. nigrostriata* use crayfish burrows to gain access to the substrate for aestivation when wetlands dry (Morgan *et al.* 1998; Thompson & Withers 1999; Bamford & Bamford 2003; McDowall 2006) as they appear physically unable to burrow themselves (Thompson & Withers 1999). Beck (1985) found *G. pusilla* (in South Australia) in the substrate of dry swamps, apparently accessed through *Cherax destructor* (yabby) burrows, and observed the fish fleeing to yabby burrows when approached. However, little research exists to support their use of burrows or how they may gain access to the substrate, or where they actually aestivate. While digging for *L. salamandroides*, Berra and Allen (1989b) came across *G. nigrostriata* under leaf litter and just below the surface in sandy soils. However, Smith *et al.* (2002b) dug a transect 2 m long by 60 cm deep through a dry wetland in Melaleuca Park known to contain a *G. nigrostriata* population, but did not find any fish. Lento-corral experiments by the authors have shown aestivation occurring in wetland sediments that have no obvious signs of crayfish burrows (unpublished data). Nevertheless, it is also possible *G. nigrostriata* aestivate within damp hollow rushes, tree roots or logs, similar to *Kryptolebias marmoratus* (mangrove killifish) (Taylor *et al.* 2008). Pen *et al.* (1993) suggested *G. nigrostriata* aestivate as a survival mechanism, given the temporary nature of their preferred habitat, although, how long they can survive while aestivating is also unknown.

Threats

Galaxiella nigrostriata are listed with a number of local, national and international organisations: 'Priority 3' (Taxa with several, poorly known populations, some on conservation lands) with the West Australian Department of Environment and Conservation, 'Restricted' with Australian Society of Fish Biology and 'Lower Risk-near threatened' with the International Union for Conservation of Nature (Wager 1996; ASFB 2007; DEC unpublished data 2008).

The main threats likely to affect continued *G. nigrostriata* population survival can be grouped into two types: climate change and habitat modification and destruction. It has been estimated that rainfall in south-west WA will continue to decline, over 40% by 2070 and evapotranspiration will increase (Watterson *et al.* 2007), which will affect wetland hydroperiod through decreased run-off and reduced groundwater recharge. Excessive anthropogenic groundwater extraction can cause unseasonal or extended dry periods in wetlands and decreasing groundwater levels could induce acidification through acid sulphate soils (Smith *et al.* 2002b; Horwitz *et al.* 2008). Wetlands will also be affected by a predicted rise in mean temperatures which will lead to an increase in evapotranspiration in south-west Western Australia (Watterson *et al.* 2007).

A number of land use practices have directly or indirectly caused the loss of up to 80% of wetlands on the SCP, such as filling or draining for agriculture, urbanization and roads, forestry, dams and other such infrastructure, mineral and quartzite sand mining under wetlands (Seddon 1972; Balla 1994; Davis & Froend 1999; Smith *et al.* 2002b). Some seasonal wetland habitats have been excavated when dry with the soil used for fill, or the dry pools filled in during road maintenance, or protected reserves undergo a change in land tenure and are no longer protected from agriculture, mining or other habitat altering activities (Trayler *et al.* 1996; Morgan *et al.* 1998). Furthermore, altered wildfire seasons and prescribed burning practices can cause organic-rich sediments in seasonal wetlands to burn for long periods, killing fish that may be aestivating within the substrate (Trayler *et al.* 1996; Semeniuk & Semeniuk 2005; Horwitz *et al.* 2008). In some areas, an increase of salinity

degrading water quality in rivers and wetlands has been caused by massive historical land clearing (Halse *et al*. 2003).

Introduced exotic fish species may impact upon native species through competition for food, aggressive/predatory behaviour that causes displacement, injury or death and by introducing disease (Becker *et al*. 2005; Rowe 2007; Marina *et al*. 2008). For example, introduced *Gambusia holbrooki* (mosquitofish) similarly prefer the shallow still water of wetlands and may show aggressive behaviour (fin-nipping) toward co-habiting species, particularly when water temperature is over 20°C (Morgan *et al*. 2004; Rowe 2007). However, the extent of aggressive behaviour or displacement from a niche is unsure. One report shows 100% mortality of *G. nigrostriata* caused by aggressive *G. holbrooki* (Griffiths 1972), while another study reported native *Hypseleotris* sp. 5 (Midgley's gudgeons) probably competing with *G. holbrooki* for food (Stoffels & Humphries 2003). Other authors disagree about the impact *Gambusia* have on galaxiid species (Ling 2004; Becker *et al*. 2005). One advantage *G. nigrostriata* have over introduced species is the ability to aestivate during dry periods. Exotic (and most native) species known to Western Australian wetlands cannot aestivate, therefore die or leave an area that dries. However, exotic species could still have a deleterious effect by attacking *G. nigrostriata* populations as water subsides, niche habitats in the water column disappear and competition for food and space increase.

Taxonomy and Nomenclature

The common name black-stripe minnow has been widely used since it was first coined by Shipway in 1953. However, some reports since the mid 1990's have used the name black-striped jollytail (EPA 2005; Coffey Env. 2009; MBS 2009), apparently referring to articles by Bamford *et al*. (*e.g.* Bamford & Bamford 1998). Mike Bamford introduced the jollytail name to replace minnow so they would not be confused with the true minnows (M. Bamford, Bamford Consulting Ecologists 2009, pers. comm.) which belong to the family Cyprinidae and do not necessarily represent only small fish (Berra 2007). More recently an official common name change from black-stripe minnow to black-striped dwarf galaxias has been accepted and published by a conglomeration of government and industry bodies (Yearsley *et al*. 2006).

Due to its similarities with the *G. pusilla*, *G. nigrostriata* was originally described as *Galaxias pusillus* ssp. *nigrostriatus* by Shipway in 1953 from specimens collected near Albany, WA (Shipway 1953). Whitley listed it as a separate species in 1964 and it was declared by Scott in 1971 as *Brachygalaxias nigrostriatus* (Whitley 1964; Scott 1971). McDowall formally identified it as belonging to the new genus *Galaxiella* in 1978 as *Galaxiella nigrostriata* (McDowall 1978). Misidentification has occurred in the past by confusing *G. nigrostriata* with *G. munda* (McDowall & Frankenberg 1981), particularly during the juvenile stage prior to the development of their unique stripes (Allen *et al*. 2002). This confusion led Berra and Allen to publish a paper examining the differences between the two species, the most conspicuous being the origin of the dorsal fin in relation

to the anal fin (Berra & Allen 1989a). It is possible other records are incorrect, as even today researchers have difficulty identifying the two species in the field due to intermediate morphological characters existing in juveniles (D. Galeotti 2009, pers. obs.) and genetic analysis is recommended to confirm their identification (S. Beatty, Centre for Fish and Fisheries Research, Murdoch University, 2009, pers. comm.)

However, little work has been done on the genetics of *G. nigrostriata*. Waters *et al*. (2000) examined phylogenetics of Galaxiidae using mitochondrial DNA (mtDNA) (cytochrome *b* and 16S rRNA) to examine Gondwanan relationships within the family. They suggested *G. munda* is more closely related to *G. pusilla* than *G. nigrostriata*, even though *G. pusilla* occur *ca*. 2,000 km away. It has been suggested that their origins are from the same location, *i.e.*, *Galaxiella* dispersed either from eastern Australian to the west, or vice-versa (Chilcott & Humphries 1996). This may have been possible when more rivers existed as seas transgressed the continent several times from the Eocene to mid Miocene (*ca*. 55–15 Ma) (Unmack 2001). The most recent time period that freshwater fish might have migrated from east to west may have therefore been *ca*. 5 Ma, at the end of the Miocene (Unmack 2001)

Smith *et al*. (2002a) used allozyme electrophoresis and morphometric analyses to assess relatedness between populations in Melaleuca Park and two populations near Northcliffe. They determined there was low genetic diversity near Northcliffe (3% polymorphism) while the population at Melaleuca Park was monomorphic, and that isolation had caused minor morphological differences between populations, specifically larger head lengths and shorter caudal peduncle lengths at Melaleuca Park. *Galaxiella nigrostriata's* whole mitochondrial genome has been mapped and added to Genbank by Miya *et al*. (unpublished data) and is freely available for researchers (Accession # NC_008448; see Benson *et al*. 2008). To further assess the genetic differences between *G. nigrostriata* populations, it has been suggested mtDNA analysis may provide a more accurate measure than allozyme electrophoresis (D. Morgan, Centre for Fish and Fisheries Research 2009, pers. comm.). The use of mtDNA may allow the path of dispersal to be more accurately mapped, and furthermore, mtDNA analysis may help determine how divergent the known populations are, *i.e.*, if they are genetically separate populations or subspecies. If the populations are genetically identical then deliberate translocations could occur between them to restock diminishing populations or rehabilitated wetlands.

Discussion

The information contained in this review provides information on many aspects of *G. nigrostriata* required to make informed decisions regarding their conservation management. However, some sections suggest areas that require further research is required, particularly aestivation and genetics. *Galaxiella nigrostriata* distribution appears to have been reduced, as indicated by historical reports that described their range as far as the towns of Esperance to the east and Gingin to the north. Fortunately the reduction is due to data entry

errors and going by the recent discovery at Lake Chandala further populations may still be waiting to be discovered. However, it is unlikely their range will extend further outwards; rather small remnants may possibly be found within their known range boundaries.

Since *G. nigrostriata* spend potentially half of their life cycle in aestivation, it begs the question why is so little known about this life phase, especially with a drying climate and increasing pressure on groundwater resources affecting the hydroperiod of wetlands where they live. Certainly, a greater understanding of aestivation requirements could increase *G. nigrostriata's* chances of survival in the challenging times ahead (re: climate change). Even though research in this area is lacking, land managers can still be mindful of how their activities may impact wetland ecosystems.

To enable *G. nigrostrinta* to survive into the future a number of management options may be considered. Protection of habitat and surrounding areas may be achieved by continuing existing and creating new nature reserves to encompass wetlands and provide substantial buffer zones. Where *G. nigrostriata* are found in degraded habitats, rehabilitation and a change in land use may be required. Reintroductions may allow rehabilitated wetlands to be restocked to widen *G. nigrostriata's* geographic range. To further assist *G. nigrostriata's* survival prospects, physical barriers such as bunds may be built to prevent exotic species entering neighbouring un-infested wetlands from permanent rivers or streams (Galeotti *et al.* 2008). Continued effort to raise public awareness about the impact of releasing exotic species into natural habitats will also help, not just *G. nigrostriata* but the survival of many other native species as well.

As genetic analysis techniques become quicker, easier and cheaper, further work in this field could help mitigate species confusion while simultaneously examining population genetic structure. Analysing mitochondrial DNA from specimens at each remnant population and the more widespread southern populations would give the most comprehensive overview of current or past genetic connectivity (McGlashan & Hughes 2001; Davey *et al.* 2003). If northern and southern *G. nigrostriata* populations show little divergence then they may all be managed in similar ways. However, a finding of genetically divergent populations may justify applying a higher conservation status and more intensive management of each sub-population (Ling *et al.* 2001; Cook *et al.* 2007; Phillips *et al.* 2007).

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The effect of the aerodynamic behaviour of flakes of jarrah and karri bark on their potential as firebrands

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Abstract

Spotting, the process by which new fires are ignited ahead of bushfires by firebrands transported by convection and wind, is a significant problem for fire suppression, and potentially, for fire crew safety. The magnitude of the potential problems caused by spotting is determined by many factors, notably spotting distance and spotfire numbers. This paper explains the notoriety of two Western Australian forest eucalypts, jarrah (E. *marginata*) and karri (E. *diversicolor*), in terms of bark aerodynamic characteristics and likely firebrand yield.

Terminal velocity, the equilibrium falling velocity, and potentially, gliding behaviour, determine how high a particle is likely to be lofted for given convection strength, and how far it will travel for a given height and wind conditions. Particles with low terminal velocities can potentially be lofted to greater heights and transported longer distances than those with greater terminal velocities. The gliding and spin behaviour of shed flakes of bark were observed during tower drops, and their terminal velocities derived from fall time.

Terminal velocity varied between 2.5 and 8 m s^{-1} and is shown to be a function of the square root of surface density (mass/projected area) of the sample, the amount of spin during free-fall, and bark shape. Bark flakes which showed rapid spin had terminal velocities up to 18% less than those of non-spinning flakes. The measurements indicate that many of these flakes could be lofted in the convection plumes of low to medium-intensity fires, such as those with fire-front intensities between 0.5 and 2.5 MW m^{-1}. Aerodynamic characteristics which would make these bark flakes effective firebrands appear to be their low terminal velocities, rather than their ability to glide.

Observed differences in spotting behaviour between the two species are their spotting densities and maximum spotting distances. These differences are not wholly explained by their measured differences in free-fall behaviour, but will more completely be explained by differences in the numbers of detachable flakes, their ease of ignition and their combustion characteristics during flight.

Keywords: bushfire; firebrands; terminal velocity; spotting; coefficient of drag; surface density.

Introduction

The phenomenon of spotting, where pieces of burning material, firebrands, are lofted by the convection of a bushfire to start new fires down wind (McArthur 1967, Tolhurst and MacAulay 2003), is the main characteristic of forest fires that determines whether or not the fire can be suppressed (McCarthy and Tolhurst 1998). Potentially, spotting can lead to entrapment and expose fire crews to grave danger. The worst cases of spotting behaviour in the world both in terms of distance and spotfire concentration occur in Australia, and this has been attributed to the aerodynamic and combustion characteristics of eucalyptus bark (McArthur 1967, Cheney & Bary 1969, Luke & McArthur 1978).

Terminal velocity and shape are important characteristics of potential firebrand material that determine if it will be lofted in a bushfire plume (Tarifa *et al.* 1965, 1967, Lee and Hellman 1969). Particle terminal velocity is its equilibrium falling speed in still air, and in order to be lofted by a fire, must be less than plume updraft velocity. The updraft velocities modelled for plumes from line fires with intensities of 0.5 MW m^{-1} and 2.5 MW m^{-1} are 4.0 m s^{-1} and 6.9 m s^{-1}, respectively (Raupach 1990). These intensities correspond to a low-intensity fire at the upper limit recommended for prescribed burning, and a medium-intensity fire at the threshold at which direct suppression by bulldozers and aerial attack may fail.

There is considerable literature on the terminal velocities of prepared and natural wood samples (Tarifa *et al.* 1965; 1967, Muraszew 1974, Muraszew *et al.* 1975; 1976, Muraszew & Fedele 1976, Albini 1979) but little on bark (Muraszew *et al.* 1976, Clements 1977, Ellis 2000).

Terminal velocity can be obtained in five ways:

- derived from a standard drag relationship; or

- derived from measurements of drag vectors of tethered particles for a range of constant horizontal air velocities (Muraszew 1974, Muraszew *et al.* 1975, Tarifa *et al.* 1965, 1967); or

- directly measured for untethered particles in a vertical wind tunnel (Ellis 2000); or

- estimated from images which show fall relative to reference points (Clements 1977); or

- calculated from drop time (Clements 1977).

During free-fall objects tend to orient themselves so that their maximum projected area (A) is normal to the relative airflow (Tarifa *et al.* 1967), and at their terminal velocity, mass forces equal drag forces. Terminal velocity (*w*) is proportional to, the square root of surface density (*m/A*) and designated '*α*' here, and inversely proportional to the square root of coefficient of drag ($C_d^{0.5}$). Determining terminal velocity using a drag relationship requires the measurement of particle mass, projected area and the value for coefficient of drag. The last is dependent on shape, velocity, surface roughness and ambient turbulence and, for standard shapes, can be obtained from engineering tables (Marks 1951). However, firebrands are typically irregular in shape, with rough surfaces, and their projected area will vary if they gyrate during flight. Hence, deriving accurate values for terminal velocity using a standard drag relationship can be problematic. The second method requires very accurate measurement and the assumption that the particle will have a constant orientation during flight. In a vertical wind tunnel, many untethered particles such as bark flakes have a horizontal vector of velocity, due to glide, which results in impact with the walls. The fourth method is also difficult with particles which glide. The drop method allows observations for a limited time of particles which are free to gyrate naturally, and a simple calculation of terminal velocity, and was adopted for this study.

The aim of this study was to compare the terminal velocities, flight behaviour and likely firebrand yield of bark of two species of eucalypt with different bark physical characteristics and spotting behaviour, karri and jarrah.

The shed bark of karri (*Eucalyptus diversicolor* F. Muell.), a gum bark type, is a supposed agent of long-distance spotting to several kilometres (McCaw 1992, White[1] *pers. comm.* 1996). Karri has gum bark which decorticates seasonally in thin irregular flakes which can be more than 1000 mm long. Mature karri forest produces about 1.5 t ha^{-1} of bark fall (O'Connell and Menagé 1982), and at any given time an unknown proportion of this would be loosely attached to the trunk or branches, and thus represent potential firebrands.

Jarrah, (*Eucalyptus marginata* Don ex Smith) has a fibrous bark type, is notorious for intense short-distance spotting to tens of metres, and less frequent spotting to one or two kilometres (McArthur 1967, Gould *et al.* 2008). Jarrah does not decorticate seasonally and large quantities of loosely attached flat or curved flakes of fibrous bark, typically up to 300 mm long, but occasionally more than 1000 mm long and 100 mm wide, accumulate on long-unburnt boles and branches. Medium-intensity fires of about 3 MW m^{-1} burning in mature northern jarrah forest consume between 6 and 8 t ha^{-1} of bark from the trunks, (Gould *et al.* 2008), and an unknown proportion of this would become firebrands.

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Methods

Bark samples

Shed samples found at the base of about six karri and jarrah trees were collected respectively from the Manjimup and Nannup areas in Western Australia. Typically, karri flakes were curled tangentially and were irregular cylindrical or curved pieces. Typically, the jarrah flakes were more uniform in shape than those of karri, and were approximately rectangular and flat, or slightly curved longitudinally. Twenty-two karri and 27 jarrah samples were considered a sufficient number to capture variation.

Samples were weighed fresh and their length to width ratio (*L:W*) calculated. Each flake was placed on a sheet of paper in its estimated flight orientation and the projected area traced, cut out and weighed. Scanning was not used because of the curvature of the bark. Area *A* was calculated from the known mass per unit area for the sheet of paper. The root of surface density (*m/A*) was then calculated.

Drop tests

Bark samples were oriented such that their flat or convex surface faced the ground and dropped from a 22.7 m mobile tower in calm conditions and their fall time recorded using a stopwatch. The flight behaviour for each sample was subjectively categorized according to how rapidly they rotated while falling. Samples that rotated rapidly about an imaginary axis perpendicular to their flat surface or rapidly about their longitudinal axis were categorized 'Spin'. Those samples that showed no spin or rotated slowly were classed as 'No-spin'. 'Spin' and 'No-spin' were ascribed the values 1 and zero, respectively. The occurrence of spiral movement was noted and the diameter of the spiral estimated visually. The terminal velocity (*w*, m s^{-1}), termed observed terminal velocity, was calculated using Equation 1 (Clements (1977);

$$w = \frac{gt - \sqrt{g^2 t^2 - 4gy\ln 2}}{2\ln 2} \qquad \text{Eqn 1}$$

where *g* is acceleration due to gravity (9.8 m s^{-2}), *t* is the fall time (s) and *y* is the height (m) from which the sample is dropped. The dimensionless coefficient of drag (C_d) for each sample was then derived using a standard approximation of a drag relationship for falling objects (Equation 2),

$$w = \left(\frac{2gm}{C_d A \rho_a} \right)^{0.5} \qquad \text{Eqn 2}$$

where *w* is terminal velocity obtained from Equation 1, *m* is mass (kg), *A* is the maximum projected area (m²) which is the area normal to the airflow, and ρ_a is the density of air (1.27 kg m^{-3} at the site).

Data analysis

Initially, the data was plotted to show the significance of root of surface density (*α*) as a determinant of terminal velocity. Subsequently, correlation and anova were used to determine if there were additional explanatory

Table 1

Length, length to width ratio (L:W), mass, projected area and square root of surface density of the bark samples. Mean (in bold), standard deviation, and range.

Species	Length (cm)	L:W	Mass (g)	Projected area (cm²)	Root of surface density (kg$^{0.5}$ m^{-1})
Karri (n=22)	**36.18 ± 11.75** (17.5–63.0)	**11.71± 6.27** (5.1–26.5)	**14.70 ± 9.77** (4.3–40.3)	**98.38 ± 58.90** (18.7–213.11)	**1.25 ± 0.28** (0.79–1.85)
Jarrah (n=27)	**27.22 ± 9.38** (12.0–46.0)	**11.27 ± 5.86** (2.0–30.0)	**8.88 ± 10.93** (0.85–42.00)	**77.81 ± 67.47** (14.13–267.10)	**0.96 ± 0.29** (0.53–1.79)

variables for observed behaviour. Linear regression was used to obtain models for terminal velocity.

Results

Bark morphology

Bark morphology is described in Table 1.

Sample gyration

All samples appeared to assume an attitude of maximum drag, where the maximum surface area was presented to the relative wind (ie facing the ground), whatever their initial orientation. Most samples established a stable flat spin which could be fast or slow. Nearly all samples described a spiral glide but no samples glided in one direction for the duration of their flight. During the 22.7 m drop, the maximum amplitude of spiral flight in the horizontal plane, observed from above, was estimated to be less than 10 m.

Explanatory variables

The correlation matrix for measured bark variables and observed free-fall behaviour is shown in Table 2.

Correlations between mass and area, length and area and length and width occur because these variables tend to be linked via sample size. The coefficients also indicate that karri and jarrah samples differ in mass, α, length, and in observed spin. Terminal velocity appears to depend on mass, α and spin, and differs between species. Spin differs between species and is weakly associated with mass and L:W, and more strongly associated with terminal velocity and the coefficient of drag. Similarly, the coefficient of drag is associated with amount of spin observed, terminal velocity and L:W.

Significance of root of surface density

Figure 1 plots terminal velocity (w) versus the square root of surface density (α), indicating species and 'Spin', and Equation 3, which was obtained using constrained linear regression.
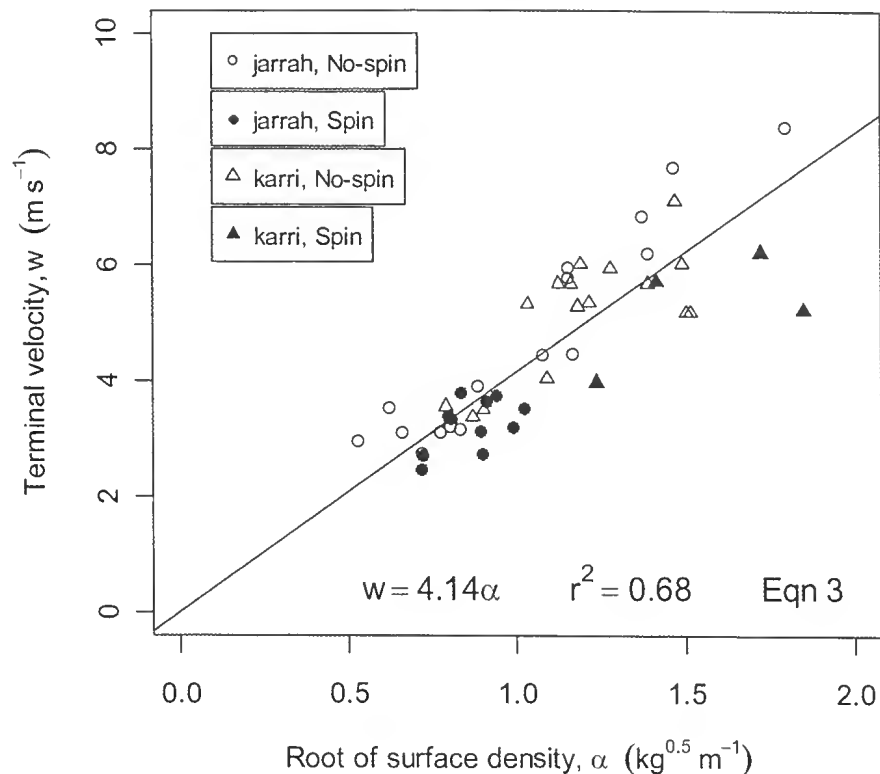

Figure 1. Relationship between the terminal velocity of shed flakes of karri and jarrah bark and the square root of surface density of each piece, indicating samples which displayed Spin during flight. Equation 3 describes the relationship between terminal velocity and the root of surface density.

Table 2

Correlation coefficients for the measured bark variables, observed spin behaviour, observed terminal velocity calculated using Equation 1, and the coefficient of drag derived using Equation 2. Values in bold are referred to in the text.

	Species	m	A	α	L	W	L:W	w	Spin
Mass (m)	**-0.27**	1.00							
Area (A)	-0.16	0.76	1.00						
Root surface density (α)	-0.45	0.59	0.10	1.00					
Length (L)	-0.40	0.56	**0.59**	0.33	1.00				
Width (W)	-0.12	0.75	0.85	0.16	**0.34**	1.00			
L:W	-0.04	-0.31	-0.42	0.09	0.27	-0.60	1.00		
Terminal velocity, obs. (w)	-0.35	0.60	0.15	**0.84**	0.21	0.17	-0.05	1.00	
Spin, ascribed 1 or 0	**0.24**	-0.23	-0.16	-0.08	-0.02	-0.19	**0.28**	-0.36	1.00
Coefficient of drag (Cd)	-0.05	-0.05	-0.03	0.16	0.15	0.01	**0.21**	**-0.37**	**0.57**

The spread of values in Figure 1 indicates that the karri and jarrah samples have different ranges in root of surface density and terminal velocity, and that samples with Spin tend to have lower terminal velocities than predicted by Equation 3. However, α is shown to be a significant explanatory variable of terminal velocity.

Differences between species

More than 35% of jarrah samples exhibited Spin, and all of these had relatively low values for α. Less than 20% of karri samples exhibited Spin, and all of these were in the upper half of the range of values for α. The means and ranges of area, α, terminal velocity and derived coefficient of drag for the No-spin and Spin categories illustrate differences between species (Table 3). Differences between means were tested using a standard 't'test.

It was considered that there were sufficient differences between species to analyse them separately. For jarrah, linear regression resulted in Equation 4;

w (jarrah)   =   4.62 α –   0.74 *Spin*   Eqn 4

$r^2 = 0.89$ (s.e. = 0.38)   (s.e. = 0.22)

(P < 0.00001)   (P = 0.004)

where w is terminal velocity (m s⁻¹), α is root of surface density (kg$^{0.5}$ m⁻¹) and Spin and No-spin are ascribed the values of one and zero, respectively.

For karri, linear regression resulted in an expression which included α (p=0.0004), mass (p=0.025), Spin (p=0.037), and all four interactions (p~0.04), and with a value for R^2 of 0.66. It is likely that because the karri samples varied in shape, and hence coefficient of drag, they showed more variability in response to surface density than did the jarrah samples. In order to remain consistent and avoid complexity, and at the cost of some precision, Equation 5 was obtained.

w (karri)   =   4.29 α –   1.40 *Spin*   Eqn 5

$r^2 = 0.51$ (s.e. = 0.67)   (s.e. = 0.48)

(P < 0.001)   (P = 0.04)

For Equations 3 to 5, the intercept was not found to be significant. The coefficients in Equations 4 and 5 are not significantly different. Figure 2 plots observed terminal velocities vs terminal velocities predicted using Equations 4 and 5 for jarrah and karri samples, respectively.

Terminal velocity was adequately predicted by variables measured surface density and observed Spin (Equations 4 and 5, Figure 2).

Table 3

The mean (bold), standard deviation and range for length to width ratio (L:W), length (L), projected area (A), root of surface density (α), terminal velocity (w) and derived coefficient of drag (Cd) for the species and spin data subsets. Significant differences (standard 't' test, P < 0.05) between means of species is indicated 'a', and between categories of spin but within species, is indicated 'b'.

|	L:W	L (cm)	A (cm²)	α (kg$^{0.5}$ m⁻¹)	w (m s⁻¹)	Cd
No-spin						
Karri	**10.53** ± 5.72 (5.1–26.5)	**36.00** ± 1.55 (17.5–63.0) a	**109.17** ± 59.54 (18.7–213.1) b	**1.18** ± 0.24 (0.79–1.52) b	**5.11** ± 1.08 (3.36–7.10)	**0.85** ± 0.23 (0.58–1.33) b
Jarrah	**10.20** ± 4.79 (2.0–19.0)	**26.28** ± 9.76 (12.0–42.0) a	**76.72** ± 63.02 (14.1–216.8)	**1.03** ± 0.36 (0.53–1.79)	**4.72** ± 1.84 (2.73–8.39) b	**0.77** ± 0.21 (0.48–1.07) b
Spin						
Karri	**17.00** ± 6.68 (9.0–23.0)	**37.00** ± 14.45 (27.0–58.0)	**49.82** ± 18.90 (29.7–73.8) b	**1.56** ± 0.28 (1.24–1.85) a, b	**5.27** ± 0.96 a (3.97–6.22)	**1.39** ± 0.43 b (0.95–1.95)
Jarrah	**12.84** ± 7.09 (5.0–30.0)	**28.6** ± 9.09 (17.0–46.0)	**79.40** ± 76.64 (19.6–267.1)	**0.86** ± 0.10 a (0.72–1.02)	**3.25** ± 0.45 a, b (2.46–3.80)	**1.13** ± 0.29 b (0.74–1.66)
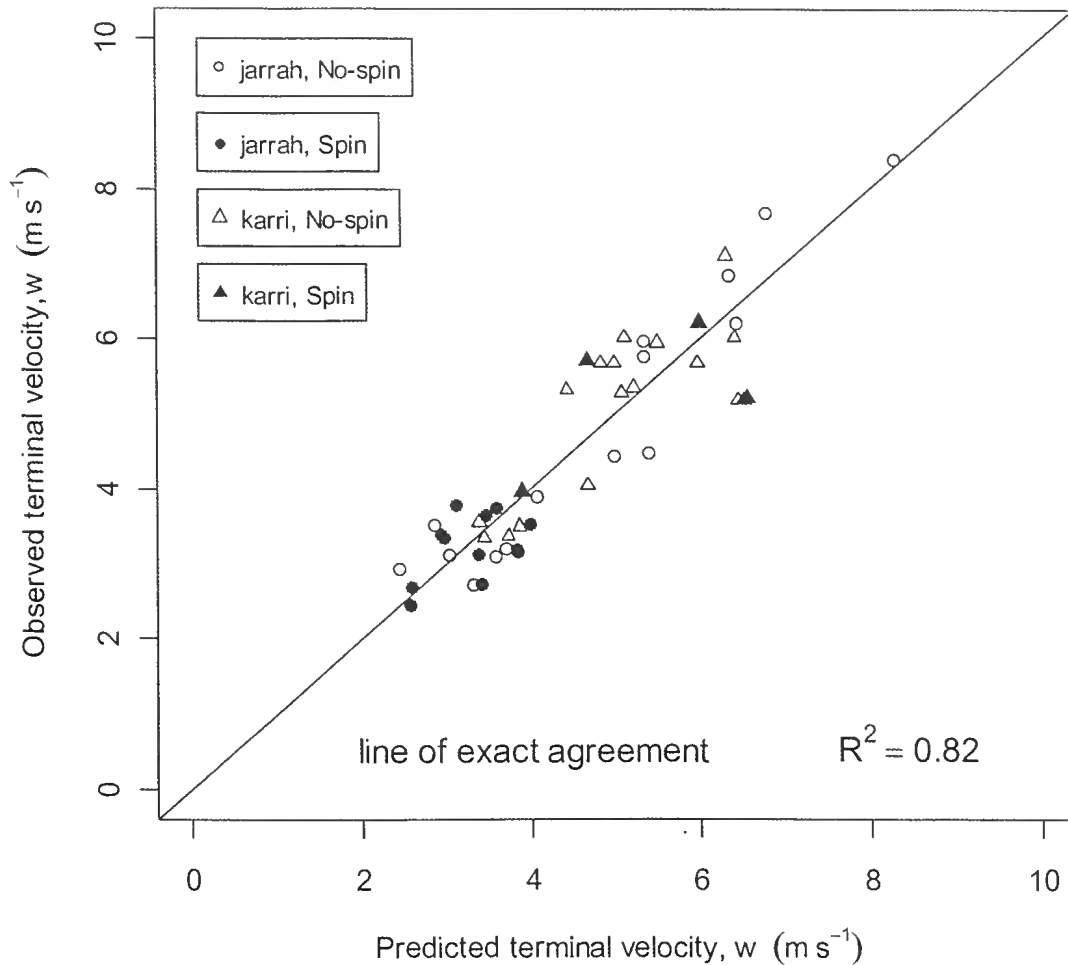
Figure 2. Observed terminal velocity vs terminal velocity predicted using Equations 4 and 5 for jarrah and karri bark samples, respectively.

Determinants of spin

Of the measured variables in Table 2, anova showed that *Species* (p=0.04), *w* (P<0.02) and *Cd* (P<0.0001) were the significant variables for *Spin*. It is argued here that Spin effectively increases drag and hence reduces terminal velocity. None of the variables for sample dimensions and mass were found to predict *Spin* although the karri samples which exhibited Spin had significantly smaller areas (Table 3, df = 17, p = 0.003), and significantly greater values for α (Table 3, df = 4, p = 0.03), than those which did not. Spin occurred rarely in karri samples, and only if α exceeded 1.24 $kg^{0.5}$ m^{-1}. Spin was more common in jarrah samples, but only if α was less than 1.02 $kg^{0.5}$ m^{-1} (Table 3).

The effect of spin on terminal velocity

Equations 4 and 5 show that Spin reduces the terminal velocity of samples significantly. For example, for a jarrah sample, Spin would reduce terminal velocity by approximately 0.74 ± 0.44 m s^{-1} (Equation 4), compared to a No-spin sample. Evidence of aerodynamic lift in this study would be indicated by significantly higher values for C_d (Guries and Nordheim 1984), as shown in Table 3. The magnitude of the effect of increased drag can be confirmed using Equation 2. The mean value for C_d of the populations No-spin and Spin were 0.82 and 1.20 (df =

20, P = 0.0006), respectively, using a standard "t" test. Increasing the coefficient of drag from 0.80 to 1.20 represents a change of about 50%, and this would result in a decrease in terminal velocity of about 18% (Equation 2).

Discussion

All samples appeared to adopt a fall position of maximum drag as previously reported (Tarifa *et al.* 1965; 1967). Although many of the flat or cylindrical samples in this study exhibited gliding descent this was invariably in a spiral pattern. From these observations it appears unlikely that such pieces of bark would continue to glide in one direction. Thus gliding would not contribute significantly to the horizontal distance gained during descent. It appears probable that bark which falls in a wide spiral could add a maximum distance of less than 10 m the horizontal distance gained by an equivalent but non-gliding sample.

However, it is possible that for a certain bark shape and wind conditions, gliding could contribute significantly.

The shape of these samples may also influence the behaviour of similar pieces within a convection column.

Lee and Hellman (1969) found that the lower drag of flat plates tended to stabilize them within a swirling convection column rather than eject them. This finding suggests that the above samples of eucalypt bark, many of which are flat to curved plates, could behave similarly.

The range of terminal velocities was similar to that established by others. Tarifa *et al.* (1967) found that the initial terminal velocities for flat wood plates ranged from 2 m s^{-1} for balsa samples to more than 14 m s^{-1} for oak samples. Clements (1977) derived a value of 5.6 m s^{-1} for undescribed samples of birch paper bark (*Betula papyrifera* Marsh.) and noted that they would remain in a flaming state at their terminal velocity. More than 20 of the 49 eucalypt bark samples tested in this study had terminal velocities of between 2.5 and 4.0 m s^{-1}. Because these terminal velocities are less than the convection updraft of bushfires of low to moderate intensity, the samples could be detached from trunks, say, and lofted above such fires. If such samples remained alight they could cause spotting beyond the burn perimeter. Most samples had terminal velocities of less than 6.9 m s^{-1}, and thus could be lofted in the convection plume of fires of moderate to high intensity.

The root of surface density (α) was shown to be the most significant explanatory variable for terminal velocity, as could be expected for a falling particle (Equation 2). Terminal velocities for jarrah samples were well-predicted using variables α and Spin (Equation 4, Figure 2), and less well-predicted for karri (Equation 5, Figure 2). This difference is probably due to the greater variability in shape of the karri samples.

The mean derived values for coefficient of drag for No-spin samples of karri and jarrah were 0.85 and 0.77, respectively (Table 3). These values are significantly less than the value of 1.17 modelled for wooden disks (Anthenien *et al.* 2006), and the standard value of approximately 1.0 for flat plates. This difference has several implications. It is likely that the derived values of Cd are valid and that they are relatively low because of the streamlining effect of the curvature of the bark samples. Alternatively, the derived values could be invalid and relatively low because the measured values for A (Table 1) overestimate the effective area presented to the airflow.

The property of *Spin* provided aerodynamic lift which significantly increased the coefficient of drag and could effectively reduce terminal velocity by almost 20%. This finding parallels work by Norberg (1973) and Guries and Nordheim (1984) on the effect of autorotation on the terminal velocities of maple samaras. Spin was common in jarrah samples, but only for samples with low surface densities.

Although this study shows some differences in free-fall behaviour between species, these are insufficient to explain differences in observed spotting behaviour. Available data on annual bark shed and bark consumption by fire are also insufficient to explain differences in spotting behaviour. Anecdotal evidence suggests that long-unburnt jarrah trunks and branches accumulate significantly more, thin, loosely attached bark flakes than do karri trunks. Such a difference, together with the fact that one third of the jarrah flakes had terminal velocities less than the minimum of the karri

flakes, could partly explain the observed differences in spotting behaviour. The rate of combustion of a firebrand affects the rate at which terminal velocity is reduced and the heat flux available to ignite a fuelbed on landing. Fast-burning firebrands will lose terminal velocity quickly and be easily transported, and, although their potential spotting distance will be reduced due to their consumption rate, will have a greater likelihood of igniting a fuelbed than slow-burning firebrands. Ellis (2000) found that for samples burning at their terminal velocities, bark of messmate stringybark (E. *obliqua* L'Her.) could have flaming times of 20 s or more, and quickly lost terminal velocity. In comparison, samples of a gum-barked type (bluegum, *E. globulus* subsp. *bicostata* Maiden, Blakely & J. Simm.) tended to have flaming times of zero or a few seconds and combust very slowly (Ellis 2000). Slowly combusting firebrands can potentially cause spotting at longer distances than fast-burning firebrands. It is likely that the combustion patterns for jarrah and karri have some similarities with the observations made for messmate and bluegum bark. It is also likely that the fibrous jarrah flakes on trunks and branches, which may be weathered for years, would ignite more easily than karri bark, which tends to be shed annually, and hence would be less weathered.

Conclusions

Most samples had terminal velocities sufficiently low for them to be lofted in the convection column of low to moderate intensity fires. The low terminal velocities of jarrah and karri bark flakes are due to low surface densities, sometimes coupled with the effect of fast spin. The lowest terminal velocities were achieved by jarrah samples, and this was due to these two properties. The karri samples showed relatively poor correlation with root of surface density, apparently because of the variability in sample shape, and hence coefficient of drag. Observed differences in spotting behaviour between the two species are their spotting densities and maximum spotting distances (Cheney and Bary 1969). Measured differences in free-fall behaviour are insufficient to explain observed differences in spotting behaviour. Additional differences between species which are likely to explain spotting observed spotting behaviour are the numbers of detachable flakes, their ease of ignition, and their combustion characteristics and pattern of loss of terminal velocity during flight.

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Diatoms in wetlands from the south-west of Western Australia: community structure in relation to pH

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Abstract

A total of 20 wetlands representing three distinct pH groups from the south-west of Western Australia were sampled over three seasons to investigate the relationship between pH and diatom community structure. Multi-dimensional scaling and analyses of similarities were used to identify differences in the diatom community structure according to geographical locations and pH groupings. Regional differences in diatom assemblages were largest between the Collie and Wagerup sites and were associated with varying pH. The largest differences among pH groups were evident between the acidic Group 1 and alkaline Group 3 sites; differences in comparisons were less defined with the circumneutral Group 2 wetlands. BIO-ENV analyses showed that pH was the variable most strongly correlated with diatom distribution patterns during each season. Potential indicator species were identified for each pH group, including *Brachysira brebissonii*, *Frustulia magaliesmontana*, *Nitzschia paleaeformis*, *Brachysira vitrea* and *Staurosira construens* var. *venter*. The results also indicated that diatoms were useful biological indicators of pH in various seasons and can therefore be incorporated into monitoring programs for pH changes in the wetlands of the south-west of Western Australia.

Keywords: acidic, alkaline, circumneutral, south-west Western Australia, wetlands, diatoms

Introduction

The acidification of surface waters has been shown to negatively impact aquatic organisms, with decreases in biodiversity and shifts in community structure commonly reported from different regions of the world (Mason 1991). A further concern for the south-west of Western Australia is the potential contamination of groundwater resources as a result of acidification (McHugh 2004). The use of an effective biological monitoring tool could form an integral part of the management strategy for threatened and acidified waters in the region. Biological monitors such as micro-algae including diatoms could provide an early detection mechanism for the impacts associated with pH decline and allow for the implementation of mitigation procedures.

The sensitivity of diatoms to pH has been clearly demonstrated by several authors such as Hustedt (1938–1939); Cholnoky (1968); Charles (1985); Stokes & Yung (1986); Round (1990) and Watanabe & Asai (2001). However, while diatoms are widely used as pH indicators (van Dam *et al.* 1981) only limited work has been carried out in Western Australia. Studies conducted by John (1993) and Thomas & John (2006) in the south-west of the state investigated diatom community structure in relation to pH but were restricted in scope.

Diatom assemblages from 10 sand-mining lakes in Capel were examined by John (1993) while Thomas & John (2006) analysed the diatom community structure of five coal mine void lakes in Collie (pH < 6). Helleren (1993) investigated diatoms as indicators of water quality in 41 wetlands of the Swan Coastal Plain and suggested several species that could potentially be used to indicate acidic waters. However, the majority of sites included in the study were alkaline and only one site was considered to be permanently acidic. In contrast, this study included 20 sites spanning three regions of the south-west. Additionally, wetlands with a greater range of pH were incorporated, including waters that have been acidified due to mining, disturbance of acid sulphate soils and organic acids.

Given that an expanding number of wetlands in Western Australia are under threat of acidification (Department of Environment 2004; McKay & Horwitz 2006) increasing knowledge on the relationship between pH and diatom communities is of growing importance. Therefore, the main objective of this study was to investigate the relationship between environmental variables and diatom communities in wetlands from the south-west of Western Australia with particular reference to pH. A further aim was to identify potential indicator assemblages or species for the different pH classifications. The study also attempted to examine seasonal variability within the distribution patterns of diatoms and assess the impact of seasonality on the effectiveness of diatoms as biological monitors of pH.

Methods

Site locations

A total of 20 sites from three localities within the south-west of Western Australia were sampled in three seasons; during the summer (December–February), winter (June–August) and spring (September–November) of 2001. Nine of the sites, mostly shallow wetlands, were situated in the Perth Metropolitan Region. Five sites were located in the vicinity of Wagerup, a predominantly agricultural area approximately 120 km south of Perth. The remaining six sites were mine void lakes created through coal-mining in the Collie Basin, a sedimentary depression approximately 200 km south-east of Perth (Table 1; Figure 1). The selection of sites from across the three localities provided a comprehensive range of pH and readily accessible sites, a pre-requisite for the seasonal sampling.

pH groupings

The selected sites were classified into three groups according to pH ranges adapted from Foged (1978): Group 1 – acidic (pH < 6.5), Group 2 – circumneutral (pH 6.5–7.5) and Group 3 – alkaline (pH > 7). As a result of the seasonal sampling regime, the pH groupings were flexible, with the number of sites assigned to each group varying in accordance with seasonal fluctuations in pH.

The pH groupings of the sites in relation to season have been presented in Table 1 and pH data for each site has been provided in Appendix 1.

Group 1 sites (pH < 6.5) were identified across the three regions and ranged from mine void lakes through to shallow seasonal wetlands. The low pH of these sites was related to factors including mining processes (Commander *et al.* 1994) and the oxidation of acid sulphate soils exposed by decreasing groundwater levels (McHugh 2004). Organic acids are also likely to have contributed, having been associated with low pH waters during previous studies in the south-west (Schmidt & Rosich 1993; Kinnear & Garnett 1999).

Group 2 sites (pH 6.5–7.5) were also identified across the three regions and ranged from shallow wetlands to mine void lakes. Land-uses in the vicinity of the Group 2 sites were generally related to urban development or agriculture.

Group 3 incorporated alkaline wetlands from two of the regions (Wagerup and the Perth Metropolitan Region). The sites were generally shallow in nature with surrounding land-uses including residential, industrial, pastoral and water collection. Substrate type and nutrient enrichment were two of the factors likely to have contributed to the alkaline pH of various Group 3 wetlands.
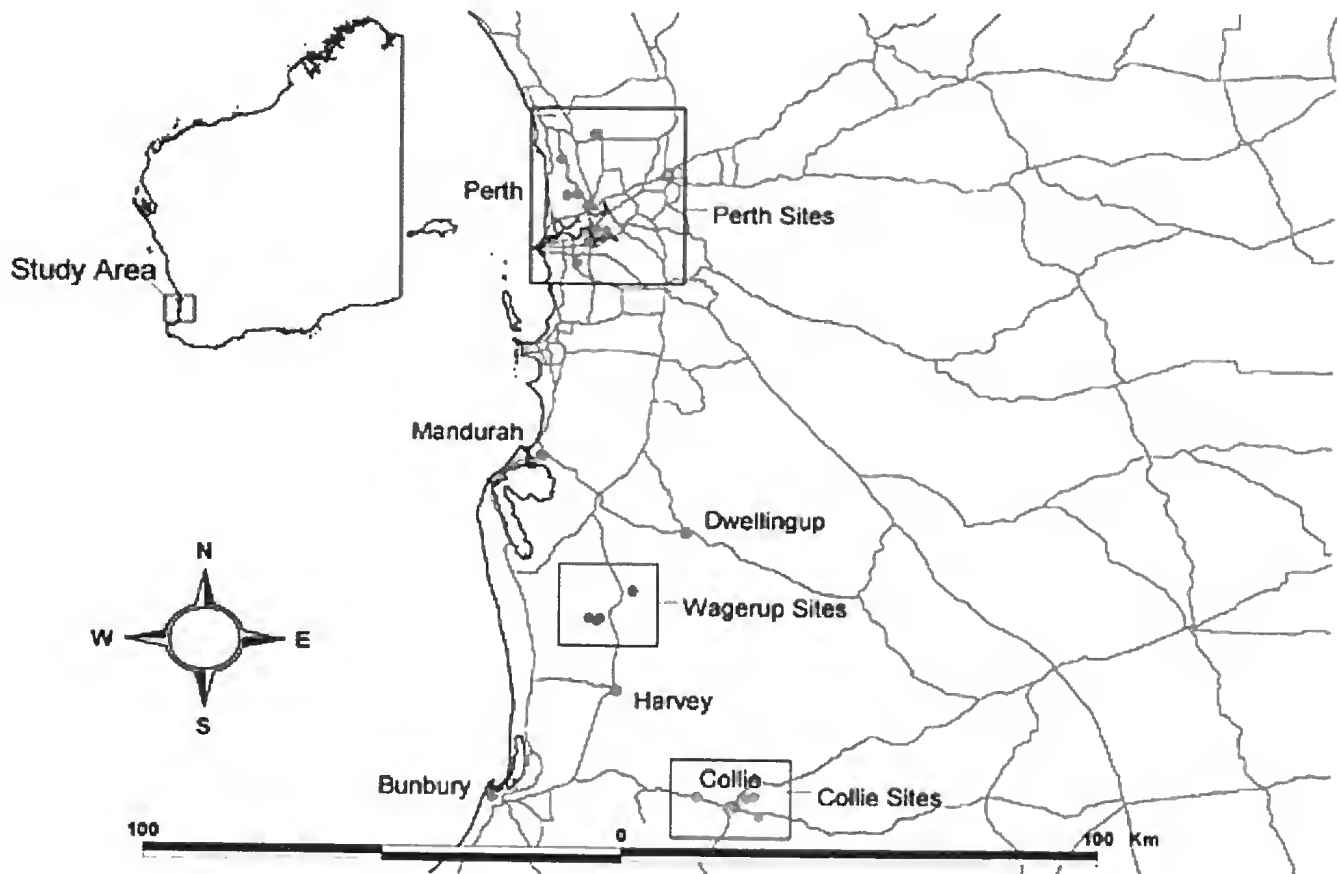

Figure 1. Location of the 20 sites in the south-west of Western Australia selected for the study, situated in the Perth Metropolitan Region, Wagerup and the Collie Basin. The closest neighbouring towns to each regional location are also shown.

Table 1

Site names, codes, locations, GPS coordinates and seasons sampled for the 20 study sites from the south-west of Western Australia. Site codes are preceded by the seasonal prefix Su to represent the summer sample, Wi to represent the winter sample and Sr to represent the spring sample.

Site Name	Site Code	Site Location	GPS Coordinates	Season	pH Group
Bibra Lake	Su1	Perth Metropolitan	32°05.19s 115°49.38e	Summer	3
	Wi1			Winter	3
	Sr1			Spring	3
Black Diamond	Su2	Collie Basin	33°20.33s 116°05.58e	Summer	1
	Wi2			Winter	1
	Sr2			Spring	1
Blind Roo A	Su3	Wagerup	32° 55.20s 115° 51.23e	Summer	1
	Wi3			Winter	2
	Sr3			Spring	1
Blind Roo B	Su4	Wagerup	32° 55.21s 115° 51.25e	Summer	3
	Wi4			Winter	3
	Sr4			Spring	3
Blue Gum Lake	Su5	Perth Metropolitan	32°02.20s 115°50.90e	Summer	3
	Wi5			Winter	3
	Sr5			Spring	3
Blue Waters	Su6	Collie Basin	33°20.24s 116°13.16e	Summer	1
	Wi6			Winter	1
	Sr6			Spring	1
Ewington 2	Su7	Collie Basin	33°20.48s 116°12.02e	Summer	1
	Wi7			Winter	1
	Sr7			Spring	1
Exelby Wetland	Su8	Wagerup	32° 55.64s 115° 52.23e	Summer	3
	Wi8			Winter	2
	Sr8			Spring	2
Gnangara Lake	Su9	Perth Metropolitan	31°46.97s 115°51.96e	Summer	1
	Wi9			Winter	1
	Sr9			Spring	1
Herdsman Lake	Su10	Perth Metropolitan	31°55.71s 115°48.03e	Summer	3
	Wi10			Winter	3
	Sr10			Spring	3
Knapping Wetland	Su11	Wagerup	32° 55.27s 115° 52.69e	Summer	3
	Wi11			Winter	2
	Sr11			Spring	3
Kurrajong Village Lake	Su12	Perth Metropolitan	32°00.76s 115°53.19e	Summer	2
	Wi12			Winter	1
	Sr12			Spring	2
Lake Monger	Su13	Perth Metropolitan	31°55.50s 115°49.45e	Summer	3
	Wi13			Winter	3
	Sr13			Spring	3
Lake Moyanup	Su14	Wagerup	32°51.41s 115°56.99e	Summer	3
	Wi14			Winter	2
	Sr14			Spring	3
Lakelands	Su15	Perth Metropolitan	31°50.55s 115°47.29e	Summer	1
	Wi15			Winter	2
	Sr15			Spring	1
Neil McDougall Park	Su16	Perth Metropolitan	32°00.45s 115°51.83e	Summer	3
	Wi16			Winter	3
	Sr16			Spring	3
Stockton Lake	Su17	Collie Basin	33°23.13s 116°13.75e	Summer	1
	Wi17			Winter	1
	Sr17			Spring	1
Stockton Tailings Pond	Su18	Collie Basin	33°23.13s 116°13.74e	Summer	1
	Wi18			Winter	1
	Sr18			Spring	1
Tusean Park	Su19	Perth Metropolitan	31°47.12s 115°51.75e	Summer	1
	Wi19			Winter	2
	Sr19			Spring	2
Wallsend Lake	Su20	Collie Basin	33°21.65s 116°09.99e	Summer	1
	Wi20			Winter	2
	Sr20			Spring	2

Environmental variables

The environmental variables of pH, electrical conductivity (µS cm⁻¹), salinity (ppm), temperature (°C) and dissolved oxygen (mg L⁻¹) were recorded from each site during the three seasons. The peripheral vegetation of each site was observed and assigned a score between 1–5, with 1 given to sparsely vegetated sites and 5 representing the most densely vegetated sites. The environmental data has been presented in Appendix 1.

Periphytic diatom sampling

Diatom samples were collected using an artificial substrate collector known as the JJ Periphytometer (John 1998). The periphytometers, fitted with 10 glass microscope slides and exposed to colonizers vertically, were employed to ensure uniform collection of diatoms. This method also avoids the problem of collecting dead cells and allows the diatom assemblages to be related to the ambient environmental conditions. Wire or 20 lb fishing line was used to secure the periphytometers to submerged structures such as a stake or tree root, ensuring the devices were well immersed. The periphytometers were retrieved after approximately 14 days of immersion, allowing sufficient time for the development of a climax community (John 1998). The slides removed from each periphytometer were placed in vials containing deionised water and preserved with the addition of 5–10 ml of Transeau's Algal Preservative (6:3:1 deionised water, ethyl alcohol and formalin).

Permanent slide preparation of diatom samples

Preparation of the diatom samples followed the techniques outlined in John (1998). The film of periphyton on both sides of the 10 slides retrieved from the JJ periphytometer was scraped into a mixture of deionised water and Transeau's Algal Preservative. Between 10–20 ml of the sample was placed in a 100 ml beaker and digested with equal amounts of Nitric Acid (70 %) and deionised water, on a hot plate set at 80 °C. After cooling, the suspension was diluted with deionised water and centrifuged for five minutes at 3500 rpm. The supernatant was decanted off to remove the acid, leaving a pellet of diatom frustules, and deionised water was added to resuspend the frustules. The centrifugation process was repeated a further four times to remove all traces of acid.

Aliquots of 100 to 1000 µl of the resuspended samples were pippetted onto glass coverslips placed on a hot plate (60 °C). The concentration varied according to the density of diatoms in the sample, with deionised water added when aliquots of less than 1000 µl were used. The even distribution of diatom frustules on the coverslips was achieved through gentle stirring of the sample. Upon evaporation, the coverslips with the dried diatom samples were inverted and gently pressed down onto clean glass slides with 4–5 drops of the mounting medium Naphrax (refractive index 1.74). The slides were placed on the hotplate to boil until the solvent present in the Naphrax had evaporated. The slides were subsequently removed, allowing the medium to cool and solidify. Three permanent slides were prepared for each sample.

Diatom enumeration

The slides were examined under oil immersion at 1000x magnification. Depending on the density of diatoms, between 100–350 diatom valves were counted and identified from each sample. Identification was to species level where possible and the relative frequencies of each taxon were determined for statistical analyses. Diatoms were identified using specialised literature (Patrick & Reimer 1966; Foged 1974; Patrick & Reimer 1975; Foged 1978; John 1983; Hustedt & Jensen 1985; Gasse 1986; Krammer & Lange-Bertalot 1986; Holland & Clarke 1989; Lange-Bertalot & Moser 1994; Ehrlich 1995; Snoeijs & Balashova 1998; John 1998; Camburn & Charles 2000; John 2000a; Siver et al. 2005). Diatom nomenclature generally conformed to Fourtanier & Kociolek (1999). Photomicrographs of diatoms were taken under oil immersion at 1000x magnification. The diatom slides have been deposited in the International Diatom Herbarium at the Department of Environmental and Aquatic Sciences, Curtin University of Technology.

Data analysis

Diatom community composition was investigated using multivariate analyses from the software package PRIMER 5.0 for Windows Version 5.2.9 (PRIMER-E Ltd 2002). Non-metric multi-dimensional scaling (MDS) ordinations (Kruskal & Wish 1978) were employed to identify groups of sites with similar diatom community structure. Species abundance data were square-root transformed and the Bray Curtis similarity measure (Bray & Curtis 1957) was used to construct similarity matrices. The significance of trends in diatom distribution was determined using one way analysis of similarity or ANOSIM (Clarke & Green 1988). A maximum of 999 permutations were used to calculate the probability of the observed values for each analysis. The BIO-ENV procedure (Clarke & Ainsworth 1993) identified the combinations of environmental variables which provided the best matches of biotic and environmental matrices. This was achieved using the Spearman rank correlation coefficient (p_s). Significance was accepted at $p < 0.05$ and $p < 0.01$.

Results

Diatom taxa

A total of 154 diatom taxa from 44 genera were recorded across the three seasons (Table 2). Over 110 taxa were identified from the summer and winter samples (115 and 113 respectively) with 106 present in the spring collection. The genus Nitzschia displayed the highest species richness in each season. Achnanthidium, Navicula and Gomphonema were also prominent although abundance varied. During the spring collection Pinnularia was also among the common genera.

Dominant taxa of the pH groups

Diatom taxa that were observed in at least two sites per wetland pH group with an abundance of at least 10 % were classified as dominant (Table 3). The species Brachysira brebissonii (Figure 2a) Frustulia magaliesmontana (Figure 2b), Navicula aff. cari and Nitzschia paleaeformis
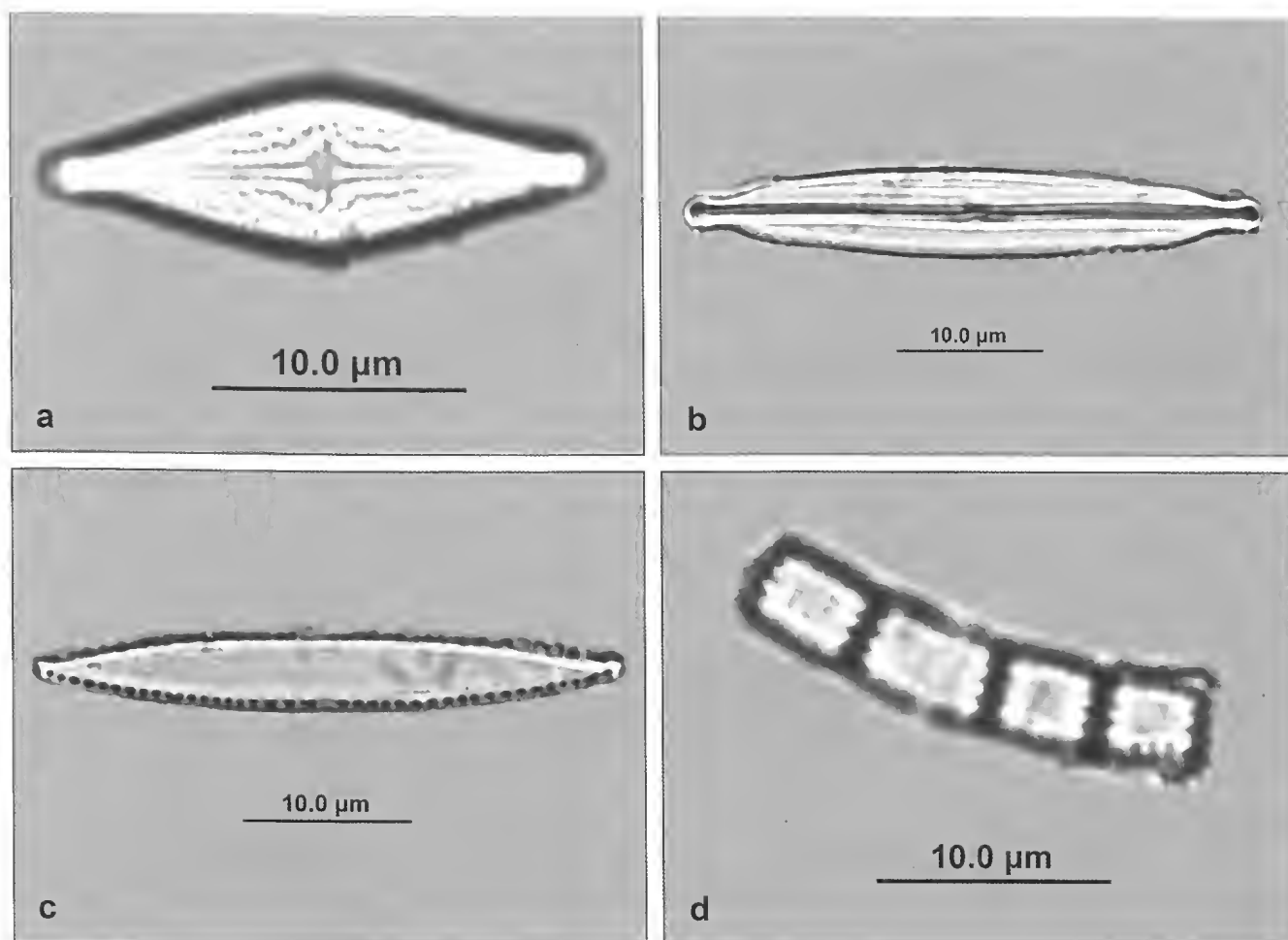
Figure 2. Examples of potential diatom indicator species a) *Brachysira brebissonii*, b) *Frustulia magaliesmontana*, c) *Nitzschia palaeaeformis*, d) *Staurosira construens* var. *venter* (chain of frustules in girdle view).

Table 2

List of genera identified from the 20 study sites in the south-west of Western Australia over the three seasons and the number of species recorded from each genus.

Genus	Species Number	Genus	Species Number
Achnanthes	1	*Gomphonema*	13
Achnanthidium	11	*Gyrosigma*	1
Amphora	6	*Hantzschia*	2
Aulacoseira	1	*Hippodonta*	1
Bacillaria	1	*Luticola*	1
Brachysira	5	*Mastogloia*	2
Caloneis	1	*Navicula*	13
Cocconeis	3	*Nedium*	3
Craticula	2	*Nitzschia*	18
Ctenophora	1	*Pinnularia*	9
Cyclotella	3	*Placoneis*	1
Cylindrotheca	1	*Planothidium*	1
Cymbella	2	*Pseudostaurosira*	1
Diadesmis	1	*Rhopalodia*	2
Encyonema	5	*Sellaphora*	2
Encyonopsis	1	*Stauroneis*	6
Epithemia	2	*Staurosira*	2
Eunotia	8	*Surirella*	3
Fallacia	1	*Synedra*	3
Fragilaria	6	*Tabellaria*	1
Fragilariforma	1	*Tabularia*	1
Frustulia	5	*Tryblionella*	1

(Figure 2c) were commonly recorded from the acidic Group 1 wetlands throughout the study. *Brachysira styriaca*, *Eunotia bilunaris* and *Eunotia pectinalis* var. *minor* also displayed a dominant presence in this group, although the seasons varied.

The dominant taxa of Group 2 displayed some overlap with alkaline Group 3. While *Achnanthidium minutissimum* and *Gomphonema parvulum* were classified as abundant in the Group 2 winter samples, both species displayed a dominant presence in the Group 3 wetlands in two or more seasons. *Brachysira vitrea* was the only taxon that occurred abundantly in the winter circumneutral wetlands alone. As none of the taxa recorded from the Group 2 wetlands during spring exceeded 10 % abundance in at least two sites, species dominance was not established.

Nine diatom taxa were classified as abundant in the alkaline Group 3 wetlands, the majority of which were rarely recorded from the other wetland groups. *Gomphonema parvulum* and *Staurosira construens* var. *venter* (Figure 2d) were commonly identified from the wetlands of Group 3 throughout the study, while species such as *Cocconeis placentula*, *Pseudostaurosira brevistriata*, *Encyonopsis microcephala* and *Nitzschia palea* were seasonally abundant (Table 3).

Table 3

Summary of the dominant diatom taxa from each pH group of wetlands sampled in the south-west of Western Australia over the three seasons. Taxa included were present in at least two sites within a pH group with an abundance of > 10 %. Group 1 represents acidic sites, Group 2 denotes circumneutral sites and Group 3 represents alkaline sites.

Taxa	Summer [1]		Winter			Spring		
	Group 1	Group 3	Group 1	Group 2	Group 3	Group 1	Group 2	Group 3
Achnanthidium minutissimum		X		X				X
Brachysira brebissonii	X		X			X		
Brachysira styriaca						X		
Brachysira vitrea				X				
Cocconeis placentula								X
Eucyonopsis microcephala		X						
Eunotia bilunaris			X					
Eunotia pectinalis var. minor	X		X					
Frustulia magaliesmontana	X		X			X		
Gomphonema parvulum		X		X	X			X
Navicula aff. cari	X		X			X		
Navicula cryptocephala					X			X
Nitzschia palea								X
Nitzschia palea var. 1								X
Nitzschia paleaeformis	X		X			X		
Pseudostaurosira brevistriata		X						
Staurosira construens var. venter		X			X			X

[1] Group 2 was excluded from the summer results due to the limited sample size.

Multivariate analyses

The ordinations of the sites based on the similarities in species assemblages displayed moderate levels of separation for each of the seasons (Figure 3a–c). Ordination of the sites according to regional location (Figure 4a–c) demonstrated that Collie sites generally clustered together, although the groupings were not discrete. In contrast, the Perth wetlands displayed two separate groupings. Five of the sites tended to cluster near the Wagerup wetlands, while the remaining four contained diatom assemblages similar to the Collie sites. The Wagerup sites grouped to the right of the axis during each season, displaying a reasonably strong separation from the Collie sites.

An overlay of symbols representing the three wetland pH groupings (Figure 4d–f) demonstrated that the acidic Group 1 wetlands were generally well separated from the alkaline Group 3 wetlands in each season. The Group 1 wetland of Blind Roo A (Site 3) was the only exception, clustering with the Group 3 wetlands during summer and appearing relatively close in ordination space during spring. The circumneutral Group 2 wetlands mostly occupied an intermediate position and displayed less defined clustering than either the Group 1 or Group 3 wetlands (Figure 4).

One way analyses of similarities (ANOSIM) conducted on the seasonal diatom data detected significant differences in the community structure of the regional location groups during each season (p < 0.05) (Table 4). The diatom assemblages of the Collie and Wagerup

Table 4

Results from one-way analyses of similarities (ANOSIM) and pairwise tests on Bray-Curtis similarities of square root transformed diatom abundance data from the regional location groups of wetlands sampled in the south-west of Western Australia. Bold type indicates significant difference (p < 0.05).

| Season	Region	R	Probability
Summer	All Regions	0.32	**< 0.01**
	Perth Metropolitan Region, Collie	0.19	> 0.05
	Perth Metropolitan Region, Wagerup	0.21	> 0.05
	Collie, Wagerup	0.78	**< 0.01**
Winter	All Regions	0.21	**< 0.05**
	Perth Metropolitan Region, Collie	0.15	> 0.05
	Perth Metropolitan Region, Wagerup	0.01	> 0.05
	Collie, Wagerup	0.72	**< 0.01**
Spring	All Regions	0.31	**< 0.01**
	Perth Metropolitan Region, Collie	0.26	**< 0.05**
	Swan Coastal Plain, Wagerup	0.12	> 0.05
	Collie, Wagerup	0.70	**< 0.01**

a

b

c
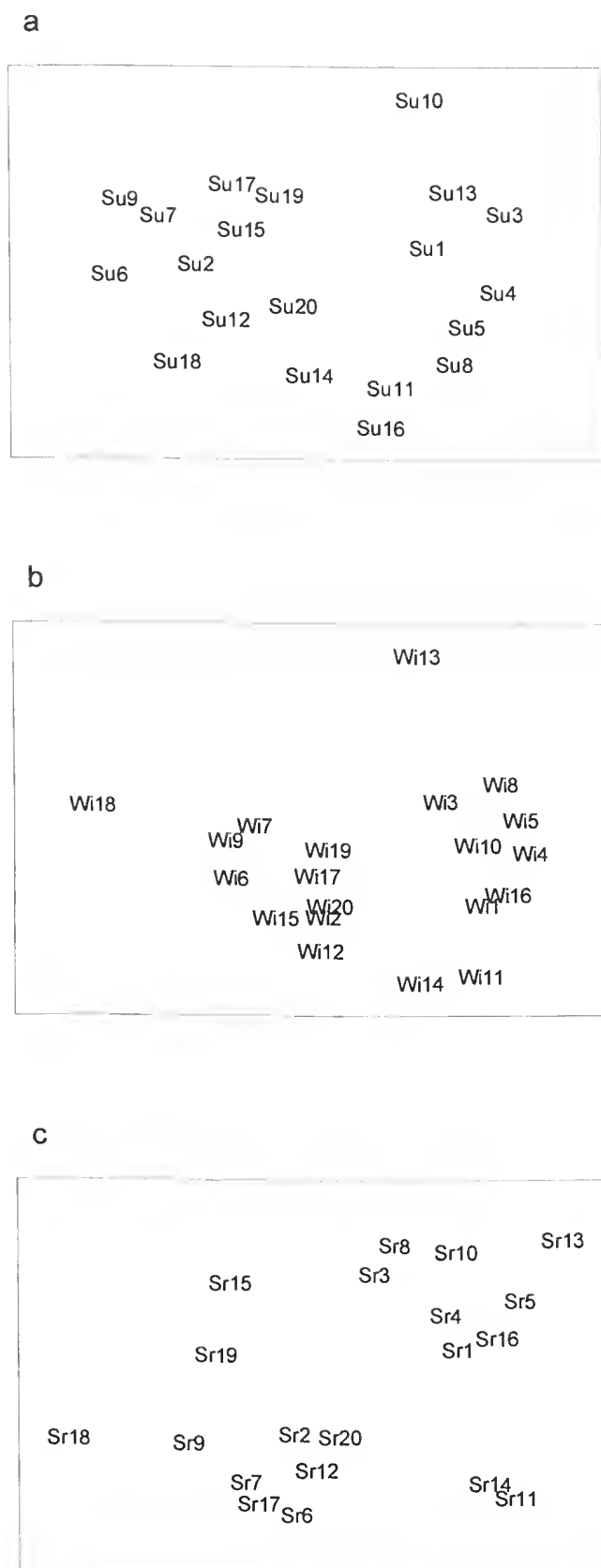
Figure 3. Two dimensional multi-dimensional scaling (MDS) ordination of square root transformed diatom abundance data with site codes superimposed. a) MDS plot of summer data, stress = 0.14. b) MDS plot of winter data, stress = 0.11. c) MDS plot of spring data, stress = 0.14. Site codes are preceded by the seasonal prefix Su to represent the summer sample, Wi to represent the winter sample and Sr to represent the spring sample.

Table 5

Results from one-way analyses of similarities (ANOSIM) and pairwise tests on Bray-Curtis similarities of square-root transformed diatom abundance data from the pH groups of wetlands sampled in the south-west of Western Australia. Bold type indicates significant difference (p < 0.05).

Season	pH Group[1]	R	Probability
Summer	Group 1, Group 3	0.64	**< 0.01**
Winter	All Groups	0.46	**< 0.01**
	Group 1, Group 2	0.25	**< 0.05**
	Group 1, Group 3	0.82	**< 0.01**
	Group 2, Group 3	0.24	**< 0.05**
Spring	All Groups	0.51	**< 0.01**
	Group 1, Group 2	0.10	> 0.05
	Group 1, Group 3	0.76	**< 0.01**
	Group 2, Group 3	0.46	**< 0.05**

[1] Group 2 not included in summer comparison due to the limited sample size.

regions were significantly different to each other in each season with relatively high R values (≥ 0.70) suggesting that the differences between these regional locations were strong. The Collie and Perth Metropolitan sites were significantly different during spring only and the relatively low R value (0.26) during this season suggested that the separation between these groups was not strong.

ANOSIM tests on the summer and winter data also established significant differences in the diatom community structure of each wetland pH group (p < 0.05) (Table 5). Comparisons of the acidic Group 1 wetlands and the alkaline Group 3 wetlands revealed the greatest differences during each season (R > 0.60). Other groups were significantly different during winter although the low R values (R < 0.50) suggest that the separation of these groups was not as strong. The spring ANOSIM generally displayed similar findings to the other seasons. The comparison between Group 1 and Group 2 was the only exception, with no significant differences detected between the diatom communities of the two groups during this season (Table 5).

The BIO-ENV analyses between environmental variables and diatom abundance data determined that the strongest correlation in each of the seasons was produced by a single parameter (Table 6). The variable of pH displayed the strongest correlation with community structure during summer and spring and achieved the same correlation as the two variable combination of pH and dissolved oxygen during winter ($\rho_s > 0.60$), supporting the relationship illustrated in Figure 4d–f.

Discussion

Diatom flora

A total of 154 diatom taxa were recorded during the study, spanning three seasons. The genera represented by the most species were consistent with the findings of previous Western Australian studies and those from other areas of Australia. For example, *Achnanthidium*, *Gomphonema*, *Navicula* and *Nitzschia* were identified as
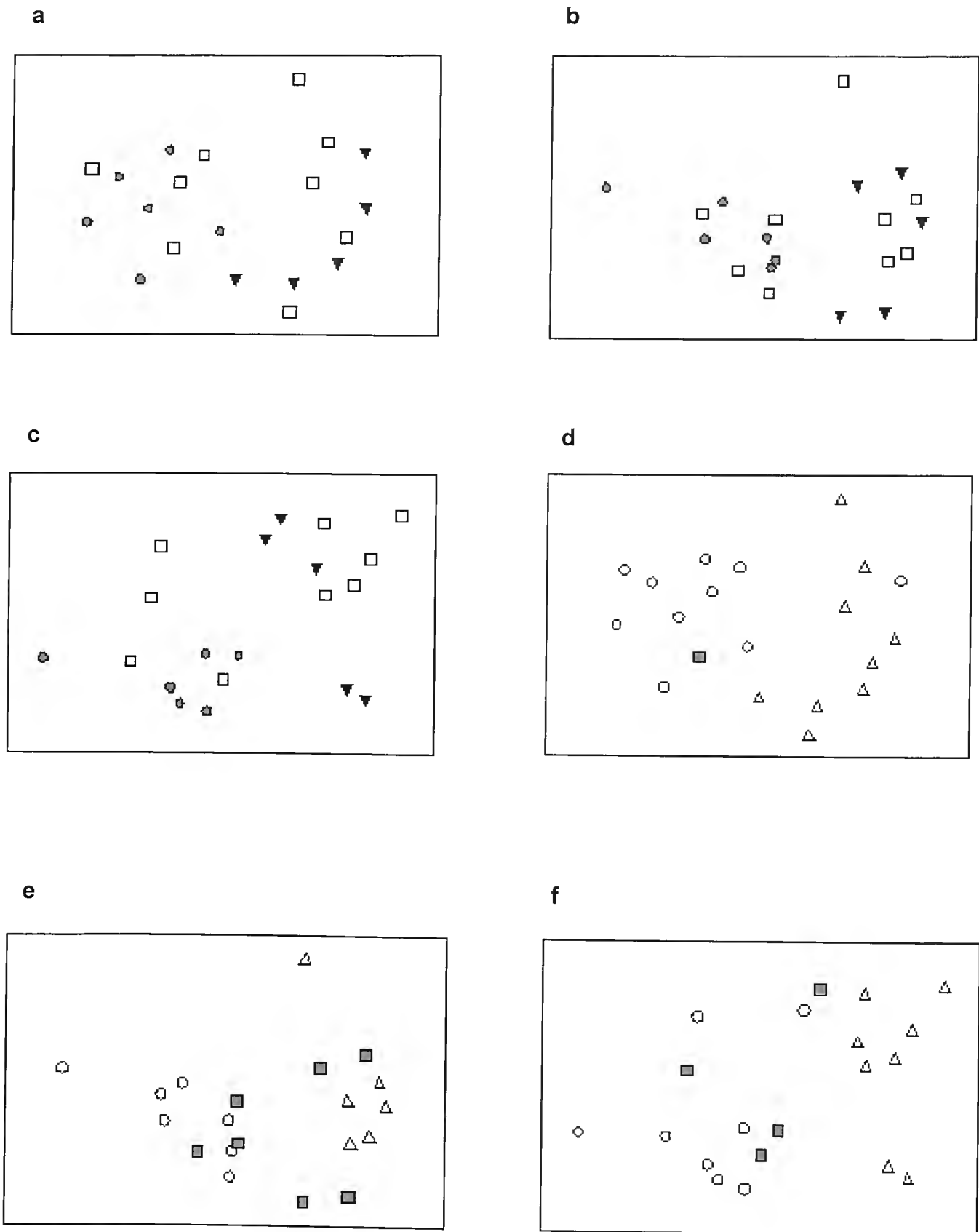
a

b

c

d

e

f

Figure 4. Two dimensional multi-dimensional scaling (MDS) of square-root transformed diatom abundance data. a) MDS plot of summer data with overlay of regional locations, stress = 0.14. b) MDS plot of winter data with overlay of regional locations, stress = 0.11. c) MDS plot of spring sample with overlay of regional locations, stress = 0.14. □ represent Perth Metropolitan sites, represent Collie Basin sites and ▼ represent Wagerup sites. d)–f) MDS plots of the summer, winter and spring data with pH groups superimposed. O represent the acidic Group 1 sites,   represent the circumneutral Group 2 sites and △ represent the alkaline Group 3 sites.

Table 6

BIO-ENV results giving the combinations of environmental variables with the highest rank correlations between the environmental variables and the square root transformed diatom similarity matrices as measured by Spearman rank correlation (ρ_s). A correlation cut-off of $\rho_s < 0.40$ was applied. The strongest correlation is presented in bold type. Veg = vegetation score, EC = electrical conductivity (μS cm^{-1}), Temp = temperature (°C), DO = dissolved oxygen (mg L^{-1}).

Season	Number of Variables	Variables	ρ_s
Summer	1	pH	**0.62**
	2	pH, DO	0.58
	3	pH, Temp, DO	0.52
	2	pH, Temp	0.52
	3	pH, EC, DO	0.51
	4	pH, EC, Temp, DO	0.49
	2	pH, EC	0.48
	3	Veg, pH, DO	0.44
	4	Veg, pH, Temp, DO	0.43
	3	pH, EC, Temp	0.43
Winter	1	pH	**0.62**
	2	pH, DO	0.62
	3	pH, EC, DO	0.55
	3	pH, Temp, DO	0.55
	2	pH, Temp	0.52
	4	pH, EC, Temp, DO	0.52
	2	pH, EC	0.51
	3	Veg, pH, DO	0.49
	3	pH, EC, Temp	0.48
	4	Veg, pH, EC, DO	0.47
Spring	1	pH	**0.63**
	2	pH, DO	0.48
	2	pH, Temp	0.45
	2	pH, EC	0.44
	2	pH, Veg	0.41
	3	pH, Temp, DO	0.40

some of the most species-rich taxa in a study on the classification of urban streams in the Perth Metropolitan Region (John 2000b). Sonneman *et al.* (2001) also identified *Nitzschia*, *Navicula*, *Gomphonema* and *Achnanthes* as the genera with the highest number of species during a study in Melbourne, Victoria. The aforementioned genera were also commonly recorded from streams in New South Wales and Victoria (Chessman *et al.* 1999).

Separation of the sites into the three wetland pH groups identified 17 dominant taxa. The alkaline wetlands of Group 3 contained the highest number of abundant species while the circumneutral Group 2 wetlands had the lowest number. This may be indicative of the small sample size of Group 2 wetlands throughout the study rather than a lack of species favouring circumneutral conditions. Alternatively, the circumneutral waters may have provided favourable conditions for a greater diversity and more even distribution of diatom taxa (Patrick & Strawbridge 1963). It is also important to note that the circumneutral or Group 2 classification had a very limited pH range (pH 6.5–7.5) in comparison to the acidic and alkaline wetland groups (pH < 6.5 and > 7.5 respectively), potentially

reducing the number of species that displayed a clear preference for circumneutral waters.

The acidic Group 1 sites were consistently dominated by diatoms including *Brachysira brebissonii*, *Frustulia magaliesmontana* and *Nitzschia paleaeformis* which could potentially be used as indicator species. The occurrence of *Brachysira brebissonii* in acidic waters has been well documented (van Dam *et al.* 1981; DeNicola 1986; Vinebrooke *et al.* 2003). Cholnoky (1968) reported that the optimum pH for the species was 5.2 and Gasse (1986) noted that a low pH appeared to be the most important ecological variable for the species. *Frustulia magaliesmontana* has previously been reported from dystrophic acidic lakes in the western region of Tasmania (Vyverman *et al.* 1996) and from acidic sand-mine lakes in Capel, southwestern Australia (pH < 4) (John 1993). *Nitzschia paleaeformis* was another taxon found commonly in Capel sand-mine lakes (John 1993). Further records of the species include a study on Japanese water bodies (pH 2.6–3.9) (Watanabe & Asai 2004) and a study on lentic heathland waters in Belgium (Denys & van Straaten 1992).

Brachysira styriaca and *Eunotia bilunaris* were among the taxa that commonly contributed to the community structure of Group 1 wetlands in at least one season. *Brachysira styriaca* has been recorded from countries including Iceland and the United States of America and appears to favour waters with pH readings of < 7 (Foged 1974; Siver *et al.* 2005). *Eunotia bilunaris* has been described by Patrick & Reimer (1966) as a frequent inhabitant of acidic waters.

Brachysira vitrea was abundant in the Group 2 wetlands only and this apparent preference for circumneutral waters is supported by the findings of other studies. Round (1990) highlighted the association of *Brachysira vitrea* with pH readings at the higher end of the spectrum (mean pH = 6.6) in a study of Welsh lakes ranging from pH 4.4–6.8. While a study of mostly acidic lakes in Florida reported that *Brachysira vitrea* was only recorded from a single lake, significantly less acidic than the other sites (mean pH = 7) (Shayler & Siver 2004). Additionally, Coring (1996) lists the taxon as being more indicative of dystrophic (humic acid) conditions rather than anthropogenic acidification.

Achnanthidium minutissimum was one of the two dominant taxa that overlapped between the circumneutral wetlands and the alkaline sites of Group 3. The species is cosmopolitan in distribution (Foged 1979) and in terms of pH preference, appears to vary according to the region. During studies in eastern Australia and New Zealand, Foged (1978; 1979) classified the taxon as alkaliphilous while Gasse (1986) commonly recorded the species in African waters ranging from weakly acidic to alkaline (pH = 6.0–8.5). Cholnoky (1968) stated that the optimum pH for *Achnanthidium minutissimum* lay between 7.5–7.8 and Patrick and Reimer (1966) found that the species occurred most frequently between pH 6.5–9.0. Similarly, in the current study *Achnanthidium minutissimum* was most abundant in wetlands with a pH > 6.5.

Gomphonema parvulum was the second taxon to occur frequently in both Group 2 and Group 3 wetlands. Similar to *Achnanthidium minutissimum*, the pH

preference of the former appears less specific than many other species. Schoeman (1973) reported that *Gomphonema parvulum* had the ability to tolerate large pH fluctuations, commonly finding it in strongly alkaline and neutral waters and recording low frequencies from some acidic waters in Lesotho, Africa. Foged (1974; 1979) and Gasse (1986) noted that the taxon generally occurs in circumneutral to alkaline waters, supporting the dominance of the species in both the Group 2 and Group 3 wetlands in this study.

Aside from *Gomphonema parvulum*, *Staurosira construens* var. *venter* was the only taxon to maintain a dominant presence in the Group 3 wetlands during all three seasons and may have potential applications as an indicator species. The species is known to be widely distributed (Patrick & Reimer 1966) and has been identified from regions including Russia (Laing & Smol 2000) and the United States of America (Camburn & Charles 2000). Previous records in Australia include streams and wetlands in Victoria (Blinn & Bailey 2001; Gell *et al.* 2002), wetlands on the Swan Coastal Plain (Helleren 1993) and the Swan and Canning Rivers in Perth (John 1983). Research from East Africa suggested that *Staurosira construens* var. *venter* favours waters of circumneutral to alkaline waters, although small numbers were also recorded from slightly acidic sites (Gasse 1986).

Cocconeis placentula, *Pseudostaurosira brevistriata*, *Encyonopsis microcephala* and *Nitzschia palea* were among the taxa abundant in a particular season. *Cocconeis placentula* was described by Cholnoky (1968) as a good indicator of moderately alkaline conditions (pH optimum of about 8) and *Nitzschia palea* was calculated to have an optimum pH of 8.4. *Encyonopsis microcephala* and *Pseudostaurosira brevistriata* have both been recorded from waters of varying pH conditions (Schoeman 1973; Hustedt & Jensen 1985), although they tend to occur most commonly in circumneutral to alkaline waters (Foged 1974; Gasse 1986).

Diatom community structure

Multi-dimensional scaling and analyses of similarities identified some significant differences in the community composition of diatoms in the different regional locations. The Collie wetlands, while not discretely grouped, tended to cluster together in ordination space and were generally well separated from the Wagerup wetlands. This was supported by analyses of similarities which detected significant differences in the diatom assemblages of the two regions during each season. The differences in community structure were likely to be partly related to pH, with the Collie lakes generally exhibiting comparatively lower pH values, attributed to past mining processes (Commander *et al.* 1994).

The Perth Metropolitan wetlands tended to separate into two groups. Gnangara Lake (Site 9), a shallow wetland with low pH linked to the oxidation of acid sulphate soils, grouped near the Collie sites as did acidic and circumneutral metropolitan sites including Lakelands (Site 15), Tuscan Park (Site 19) and Kurrajong Village Lake (Site 12). In contrast, alkaline Perth sites such as Lake Monger (Site 13), Bibra Lake (Site 1) and Blue Gum Lake (Site 5) generally clustered near the mostly alkaline Wagerup sites. Geology is likely to be

one of the factors which contributed to the alkaline nature of the Perth sites, with Lake Monger located on the limestone rich Spearwood Dune system (Lund and Davis 2000) and Blue Gum and Bibra Lakes (as part of the eastern Beeliar wetlands) bordering the Spearwood Dune system (Bennett Brook Environmental Services 2004). In addition, wetlands such as Bibra Lake and Lake Monger are eutrophic (Cheal *et al.*1993) and may display elevated pH in response to high levels of photosynthesis (Schmidt & Rosich 1993).

MDS and analyses of similarities also detected significant differences in the community structure of diatoms in the three wetland pH groups, suggesting that pH was an important factor contributing to the separation of the sites. The largest differences in community structure were evident between the acidic Group 1 and alkaline Group 3 wetlands. Dissimilarities between the dominant taxa of the two groups of wetlands further supported the differences displayed in the overall community structure.

The primary exception to the otherwise strong separation of the two groups of wetlands was the generally acidic wetland of Blind Roo A (Site 3). This site, along with other Wagerup wetlands including Blind Roo B (Site 4) was originally created through clay extraction. However, in contrast to the mostly alkaline nature of the other Wagerup sites, Blind Roo A was relatively dark in colour and had a comparatively low pH, attributed to humic acid derived from high levels of vegetative material. Despite this, the overall community composition was atypical of acidic wetlands, suggesting that variables other than pH were the over-riding factors in the diatom community structure. Taking the history of the site into consideration, it seems likely that unmeasured factors linked to substrate type may have influenced the diatom assemblages present. Additionally, the Wagerup sites are situated on pastoral land and surrounding land-use practices have potentially exposed the wetlands to impacts such as nutrient enrichment (Harper 1992). For example *Gomphonema parvulum*, a species able to tolerate a range of pH (Schoeman 1973) and known to occur in waters with high nutrient levels (Patrick & Reimer 1975; Silva-Benavides 1996; Gell *et al.* 2002; Soininen 2002), was identified from both Blind Roo A and Blind Roo B during each season, generally occurring in high numbers.

Despite some limited overlap between the dominant species of the circumneutral and alkaline wetlands (Groups 2 and 3), the overall community structure of the two groups of wetlands was found to be significantly different during both seasons analysed (winter and spring). Significant differences were also detected between the acidic Group 1 and circumneutral Group 2 wetlands during winter. However, the two groups had relatively similar species composition in spring. These similarities may have resulted from the fluctuation of sites between the acidic Group 1 and circumneutral Group 2, potentially contributing to changes in the overall community structure of the groups. Additionally, three of the four sites identified as Group 2 sites during spring were all close to the lower limit of the circumneutral classification, which may have influenced the type of diatoms present. A greater understanding of the community structure of circumneutral waters in this

pH range could be gained from the inclusion of more circumneutral sites in future studies.

The findings generally suggest that pH is an important influence on diatom distribution, in accordance with other studies including ten Cate *et al.* (1993), Battarbee *et al.* (1997) and Siver *et al.* (2004). The results of the BIO-ENV analyses further support this concept with pH being identified as the variable most closely related to diatom community structure. It should however be noted that the relatively low number of study sites may have affected the reliability of the results. Larger sample sizes generally improve the chances of successfully linking biotic and environmental patterns (Clarke & Warwick 2001). Additionally, the influence of factors other than pH must be considered. For example the BIO-ENV results showed that the combination of pH and dissolved oxygen displayed a correlation similar to that of pH alone in each season. The effect of dissolved oxygen on species assemblages was highlighted by Schoeman (1973), who listed *Achnanthidium*, *Cymbella* and *Fragilaria* as taxa that are generally abundant in highly oxygenated waters.

A further consideration is the influence of variables which were not investigated during the study. Diatom community structure is known to be influenced by factors such as nitrogen (Saros *et al.* 2003), calcium (Patrick 1945) and metals (Anderson *et al.* 1986; Hirst *et al.* 2002; Gold *et al.* 2003), the latter of which is likely to be particularly relevant given the high levels of metals such as aluminium and iron commonly associated with acidic waters (Schindler 1988; Sammut & Lines-Kelly 2000). Accordingly, future studies would benefit from the inclusion of a greater number of environmental variables.

Seasonal differences in diatom community structure

Patrick (1964) reported that diatom assemblages may vary between seasons in terms of the taxa present and their contribution to overall community structure. Accordingly, there were some differences apparent in some of individual taxa during the current study. Despite this, the acidic sites were significantly different from the alkaline sites during each season and both pH groups contained some consistently dominant species. Taxa such as *Brachysira brebissonii* and *Frustulia magaliesmontana* were dominant in the Group 1 wetlands during each season while *Gomphonema parvulum* and *Staurosira construens* var. *venter* were consistently dominant in the Group 3 wetlands. Differences between the seasons were more evident for Group 2, potentially linked to the comparatively small pH range, resulting in greater variability in the number and proportion of sites classified as circumneutral in each season.

Conclusion

The overall structure of the diatom communities generally varied between the different wetland pH groups and pH was considered to be one of the factors responsible for variation in diatom community structure between regional localities. Furthermore, the results indicate that a relatively strong relationship between diatom community structure and pH was evident in various seasons, suggesting that diatoms would be useful

biological monitors of acidification during a regular monitoring program. The study also identified potential indicator species for the various pH groups, however the application of these taxa as indicators requires further investigation.

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Appendix 1

Values for environmental variables measured at the 20 study sites from the south-west of Western Australia.

Site Name	Site Code	pH	Salinity	Electrical Conductivity	Temperature	Dissolved Oxygen	Vegetation Score
Bibra Lake	Su1	9.84	896.00	1588.00	20.40	4.64	4
	Wi1	8.48	324.00	764.00	14.90	7.50	4
	Sr1	8.23	663.00	1386.00	16.90	4.17	4
Black Diamond	Su2	5.63	132.00	325.00	31.00	5.35	3
	Wi2	5.73	193.00	538.00	12.80	7.21	3
	Sr2	5.26	195.00	447.00	19.00	8.27	3
Blind Roo A	Su3	6.45	60.30	124.80	29.30	6.76	3
	Wi3	6.64	73.80	202.50	14.80	5.42	3
	Sr3	5.86	115.00	249.00	17.70	5.72	3
Blind Roo B	Su4	10.00	242.00	473.00	32.60	7.56	2
	Wi4	9.08	187.00	495.00	15.10	5.49	2
	Sr4	9.29	187.00	395.00	21.90	10.18	2
Blue Gum Lake	Su5	9.65	944.00	1666.00	27.40	9.54	4
	Wi5	7.79	246.00	683.00	14.80	6.92	4
	Sr5	8.57	363.00	780.00	20.00	6.60	4
Blue Waters	Su6	4.03	594.00	1366.00	26.20	5.94	1
	Wi6	4.17	706.00	1866.00	12.90	7.52	1
	Sr6	3.98	686.00	1485.00	17.60	9.11	1
Ewington 2	Su7	4.25	555.00	1282.00	25.60	5.15	3
	Wi7	4.44	516.00	1381.00	12.90	7.32	3
	Sr7	4.16	637.00	1380.00	18.80	8.69	3
Exelby Wetland	Su8	8.22	151.00	302.00	32.00	6.19	2
	Wi8	7.01	154.00	410.00	15.30	4.01	2
	Sr8	7.19	201.00	423.00	22.30	7.15	2
Gnangara Lake	Su9	3.01	3140.00	5230.00	30.20	5.68	2
	Wi9	3.86	461.00	1172.00	15.50	7.30	2
	Sr9	3.59	802.00	1689.00	23.90	8.28	2
Herdsman Lake	Su10	8.88	397.00	729.00	25.40	13.50	3
	Wi10	7.66	361.00	923.00	15.60	5.02	3
	Sr10	8.04	523.00	1124.00	22.30	7.42	3
Knapping Wetland	Su11	9.46	337.00	637.00	34.60	7.26	3
	Wi11	7.28	267.00	697.00	15.60	5.14	3
	Sr11	9.30	289.00	603.00	24.20	11.03	3
Kurrajong Village Lake	Su12	6.54	165.00	316.00	26.10	9.03	2
	Wi12	6.30	111.00	315.00	16.40	5.40	2
	Sr12	6.73	177.00	392.00	20.20	8.81	2
Lake Monger	Su13	8.93	506.00	917.00	24.20	8.92	2
	Wi13	9.48	301.00	781.00	16.00	8.43	2
	Sr13	9.03	360.00	785.00	22.30	8.35	2
Lake Moyanup	Su14	8.24	142.00	284.00	30.50	4.95	3
	Wi14	7.50	104.00	281.00	14.80	6.04	3
	Sr14	8.81	168.00	355.00	22.90	10.70	3
Lakelands	Su15	6.15	1209.00	2086.00	24.80	5.67	4
	Wi15	6.73	481.00	1219.00	14.30	6.93	4
	Sr15	6.04	526.00	1125.00	22.50	8.27	4
Neil McDougall Park	Su16	9.78	270.00	503.00	20.90	11.87	2
	Wi16	7.66	44.10	130.80	15.90	6.04	2
	Sr16	8.50	78.00	179.50	19.90	7.57	2
Stockton Lake	Su17	5.53	185.00	447.00	27.10	5.21	3
	Wi17	6.45	187.00	523.00	13.10	7.47	3
	Sr17	4.59	258.00	582.00	17.70	9.02	3
Stockton Tailings Pond	Su18	3.31	451.00	1053.00	26.40	3.81	4
	Wi18	3.34	504.00	1350.00	13.00	7.64	4
	Sr18	3.12	618.00	1332.00	18.00	8.83	4
Tuscan Park	Su19	6.38	262.00	479.00	26.00	6.38	2
	Wi19	6.54	134.00	361.00	14.90	6.60	2
	Sr19	6.56	156.00	351.00	21.80	7.36	2
Wallsend Lake	Su20	6.49	177.00	430.00	25.90	5.93	4
	Wi20	6.92	179.00	503.00	12.70	7.32	4
	Sr20	6.66	195.00	447.00	19.00	8.27	4

Zooplankton from the inshore waters of Christmas Island (Indian Ocean) with reference to larvae of the red land crab, *Gecarcoidea natalis*

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Abstract

The red land crab, *Gecarcoidea natalis*, which is endemic to Christmas Island in the Indian Ocean, has an obligate marine larval phase. Surface plankton tows, using a 500 μm mesh net, were completed monthly at three sites on the north coast of Christmas Island to determine the composition, abundance and seasonal variation of the macro-zooplankton and detect the presence of red crab zoea larvae. The highest plankton concentrations were found at the end of the south-east monsoon period and, at all other times of the year, plankton settled volumes were very low, typically <0.1 ml/m³ of water sampled. Despite rearing red crab zoea obtained from spawning females, it was not possible to definitively identify them from among the wide diversity of brachyuran zoea found in the plankton samples.

Keywords: Macro-zooplankton, Brachyuran zoea, red land crab, Christmas Island.

Introduction

Christmas Island is a seamount in the Indian Ocean (10 °S 105 °E), 390 km south-west of Java, Indonesia. The island has four well-defined promontories (Figure 1) and the 73 km perimeter is characterised by steep limestone cliffs fringed by a narrow coral reef (10-50 m in width). These reefs drop off steeply and water depth increases rapidly reaching 5000 m within a few kilometres of the island.

The tropical climate is defined by a steady, dry, south-east monsoon from May-November and an erratic, wet, north-west monsoon from December-April (Clark 1994). The waters around Christmas Island are influenced by the South Equatorial Current which is fed from the east via the Indonesian Throughflow and a weaker anticyclonic gyre from north-west Australia (Wyrtki 1962; Quadfasel *et al.* 1996; Wijffels *et al.* 2002). This South Equatorial Current is strongest at the end of the south-east monsoon and weakens during the north-west monsoon when the eastward flowing South Java Current develops (Wyrtki 1962).

Marine research at Christmas Island has generally been limited to biodiversity surveys of sponges, reef building corals, molluscs, decapod crustacea, echinoderms and fishes (Berry 1988; Allen & Steene 1988; Allen 2000). There have been no studies on the plankton around Christmas Island although, during the Indian Ocean Expedition, zooplankton abundance was measured from tropical to temperate waters along a transect corresponding to longitude 110 °E (Tranter & Kerr 1967).

Of the 20 species of land and intertidal crabs that have been recorded on Christmas Island, the endemic red land crab, *Gecarcoidia natalis*, is the most abundant (Clark 1994). The current population of red crabs has been estimated at approximately 47 million (Parks Australia North 2005).

Each year, at the beginning of the north-west monsoon, millions of red crabs migrate to the ocean to spawn (Hicks *et al.* 1984). Consistent rainfall at the onset of the north-west monsoon usually results in one major spawning event while inconsistent rainfall can result in sporadic or postponed migrations and a breeding season lasting in excess of three months (Hicks 1985). The red crabs spawn in the early hours of the morning on the high tide over a period of 2–3 days between the last quarter of the moon and the new moon (Hicks 1985). Such synchronised lunar spawning has also been documented in Bermuda for a land crab of the same family, *Gecarcinus lateralis* (Wolcott & Wolcott 1982).

Red crab larvae take about 27 days to develop into megalopae which settle along the shore line for two days before returning to the land (Hicks 1985). Large-scale survival and emergence of post-larval red crabs onto the island is sporadic, usually once or twice in ten years (Clark 1994). The larval phase of the red crab is undescribed but other brachyuran crabs are known to have 2-13 zoeal stages. One gecarcinid crab from the tropical and subtropical Atlantic coast of the Americas, *Cardisoma guanhumi*, has been described with five zoeal stages and one megalopal stage (Boltovsky 1999). Studies on megalopae settlement of other brachyuran crabs have shown recruitment to be dependent on oceanographic processes, wind driven currents and tidal movements (Johnson *et al.* 1984; Garvine *et al.* 1997; Flores *et al.* 2002; Perry *et al.* 2003; Lee *et al.* 2005).

This project was designed to determine baseline data on composition, abundance and temporal variation of the macro-zooplankton in the inshore waters around
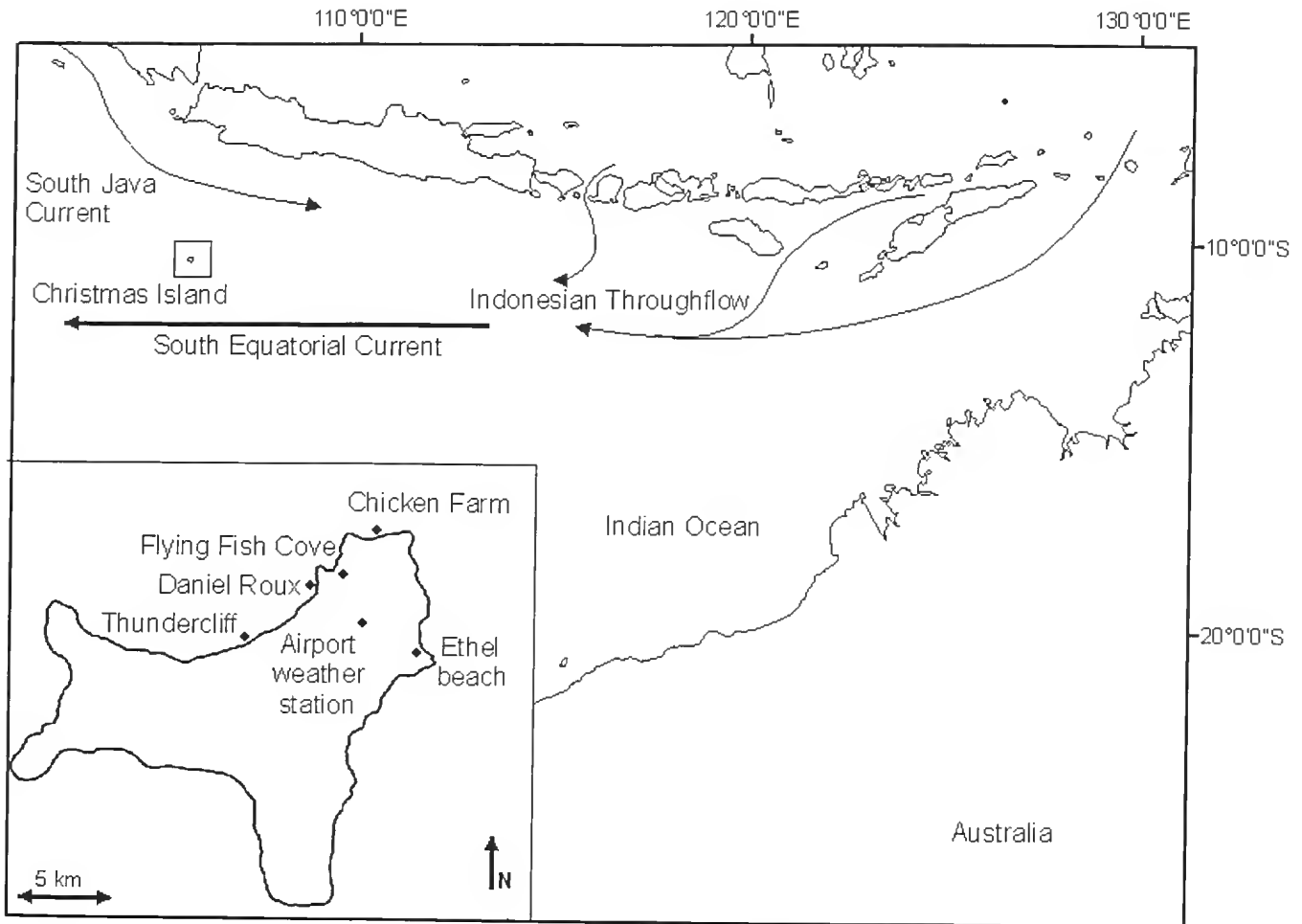
Figure 1. Location of Christmas Island in the eastern Indian Ocean. Inset shows a map of Christmas Island and indicates the sampling sites and places mentioned in the text.

Christmas Island. It was hypothesised that the abundance of plankton would be correlated with the seasonal oceanographic conditions associated with the south-east and north-west monsoons. Further, it was hypothesised that the planktonic stages of the endemic red land crab would be present in significant numbers during the spawning period over the north-west monsoon.

Methods

Environmental data

Meteorological data (1972–2006) were obtained from the weather station at Christmas Island airport through the Australian Bureau of Meteorology (BOM). The oceanographic conditions around Christmas Island were described from sea surface thermal imagery (6-day composite), altimetry (sea height) and surface drifter buoy trajectories (geostrophic current velocity and direction). These were accessed from CSIRO (www.marine.csiro.au/remotesensing/oceancurrents) and collated for the time periods around the plankton sampling trips.

Plankton sampling

Plankton sampling was undertaken close to the new moon period each month from November 2005 to December 2006 at three sites off the north coast of Christmas Island: Chicken Farm, Thundercliff and Daniel Roux Cave (Figure 1). These sites were chosen as they are adjacent to known red crab spawning areas and accessible with a small boat launched from Flying Fish Cove. Plankton was collected in daylight hours (09:00 to 12:00) using a 500 µm mesh net (0.6 m diameter, 3 m length), towed just below the surface at 1.5 knots, 30 m behind a small boat. At each site, two replicate tows were made parallel to the reef edge in water about 30–50 m deep. The volume of water filtered was determined using a General Oceanics flowmeter suspended in the mouth of the net. Sea surface temperature was measured using a YSI Model 85 multimeter at all three sampling sites. These temperatures were verified against Argo float data and satellite data from the aforementioned CSIRO website. Sampling was not conducted at Thundercliff in March 2006 and at Chicken Farm in June 2006 due to mechanical break down and bad weather, respectively.

Plankton samples were immediately fixed in 5 % formalin and transferred to 70 % ethanol after 24 hours.

Total settled volume of plankton (ml) was measured by allowing the samples to settle in graduated measuring cylinders for 24 hours. Plankton samples were examined under a dissecting microscope and counted following the subsampling method of Gibbons (2000). The plankton were identified to the lowest taxon possible and the counts were standardised by dividing by the volume of water filtered per tow to give a number per taxon per m^3.

Timing of spawning and rearing of red crab larvae

Eggs were collected from spawning red crabs at Ethel Beach (Figure 1) in January 2006 and transferred into a 50 L glass aquarium. The seawater in the aquarium was filtered through a 300 μm mesh sieve and replaced daily. As there were no facilities for culture of appropriate food organisms on Christmas Island, zoea were not fed anything additional to that occurring naturally in the seawater. To determine the developmental stages of the zoea, specimens were sampled at 12 hour intervals and fixed in 5 % formalin. This experiment was repeated during the spawning in December 2006 with extra plankton filtered from seawater added to the aquarium to supplement the food supply.

The zoea collected from the plankton samples were visually compared with those of the reared red crabs. The diagnostic features of the zoea were used to identify the zoea, i.e. arrangement of spines and telson shape. When this did not allow confident identification of red crab zoea the morphometrics (dorsal spine length and the body width) were measured using an eyepiece micrometer. Similar measurements were made on a selection of six brachyuran crab zoea removed from the plankton samples each month. In an attempt to identify red crab larvae in the zooplankton samples, the ratios of the maximum body width to dorsal spine length (the straight distance between the dorsal spine base and tip) were compared between the reared red crab zoea and those caught in the zooplankton samples. Zoea specimens were photographed using a Nikon dissecting microscope and digital camera.

Results

Environmental data

Total rainfall at Christmas Island over the project duration was relatively low, only 1379 mm over the fourteen months compared to 2483 mm which would be predicted from historical data (BOM rainfall data 1972–2006). The 2005–2006 north-west monsoon (December to April) was weak with long dry spells until April 2006 which was the wettest month. The 2006–2007 north-west monsoon brought rain in December 2006 with above average rainfall for that month.

The South Equatorial Current, as indicated by the geostrophic current velocities, was flowing weakly westward throughout the north-west monsoon periods and was frequently disrupted by eddies between the Indonesian Throughflow and Christmas Island. The current intensified during the south-east monsoon, reaching peak flows of >1 m/s in September 2006, before weakening as the 2006–2007 north-west monsoon developed. The maximum sea surface temperature

recorded during plankton sampling was in March 2006 (29.7°C), and the lowest was in September 2006 (24.5°C).

Plankton composition and abundance

Mean filtered water volume per tow at the three sites was 170 m^3 (SE ± 52). The highest settled volume of plankton (1.9 ml/m^3 of water sampled) was recorded in September 2006 (Figure 2). From January to July 2006 plankton concentrations were consistently low, typically <0.1 ml settled volume/m^3 of water sampled. Slightly higher concentrations were observed at the start of the sampling in November and December 2005 and from October 2006 to December 2006. Two way ANOVA revealed that the settled volumes of plankton were significantly affected by the sampling site ($p < 0.05$, $F_{3,2} = 34.1$) and the time of year (month) ($p < 0.05$, $F_{2,0} = 62.3$). There was also a significant interaction between the site and the time of year ($P < 0.05$, $F_{1,8} = 11.8$).

Copepods dominated the overall zooplankton composition from all sites (Figure 3) contributing 54 % (SE ± 27 %) of the individuals counted. Chaetognatha (7 %) and Cnidaria (9 %) were also consistently common. The Thaliacea were mostly salps with only a few doliolids recorded. Other Crustacea included amphipods, euphausiids, mysids, decapods, isopods, stomatopods and cumaceans. Brachyuran crab larvae were recorded throughout the year in the plankton samples at Christmas Island with a seasonal peak during the north-west monsoons (Table 1).

Timing of spawning and rearing of red crab larvae

The red crab spawning events over the 2005–2006 north-west monsoon were sporadic. The first and largest red crab spawning was around the 27th November 2005, followed by a smaller spawning event around the 26th December and

Table 1

Mean abundance of all brachyuran crab zoea each month (individuals per m^3 of water sampled) at Christmas Island during the period November 2005 to December 2006. * indicates months when red crab larvae would be expected as spawning events had been observed prior to sampling.

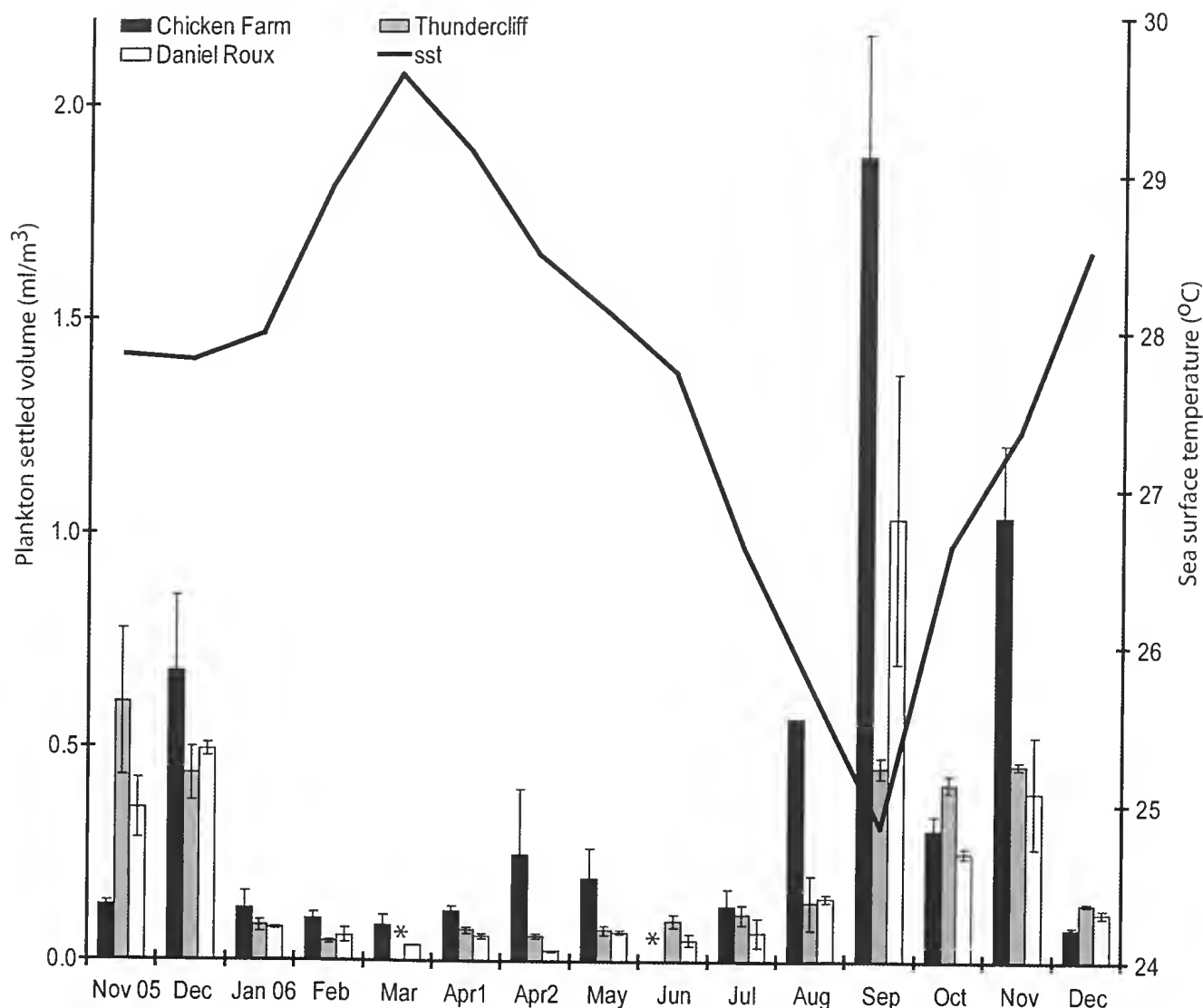|	Brachyuran Zoea (per m^3 water sampled)		
	Chicken Farm	Thundercliff	Daniel Roux
Nov	0.10	18.34	2.58
Dec*	6.09	0.18	0.47
Jan*	0.31	0.02	0.12
Feb*	0.30	0.02	0.08
Mar	0.10	no sample	0.24
Apr1	0.11	0.04	0.06
Apr2	0.15	0.01	0.17
May	0.35	0.11	0.00
June	no sample	0.03	0.25
July	0.09	0.12	0.11
Aug	0.20	0.01	0.11
Sept	0.50	0.05	0.31
Oct	0.75	0.02	0.14
Nov	1.48	3.38	0.34
Dec	0.46	1.39	0.52

Figure 2. Mean (and SE) monthly settled volumes at each site (ml of plankton /m³ of water sampled) and sea surface temperature measured at the time of sampling. * indicates that no samples were taken at Thudercliff in March 2006 or Chicken Farm in June 2006.

very small spawning events around 26th January and 27th February (C. Davies pers. obs.). During the January 2006 spawning event, eggs were collected as the female crabs spawned them into the water at Ethel Beach. The first migration of the 2006–2007 season occurred in December 2006 after the sampling and eggs were collected at Flying Fish Cove Beach as they were being spawned.

The red crab zoea from January 2006 survived for a week in the aquarium but did not moult into a second zoeal stage. Similarly, zoea from the December 2006 spawning that were reared with supplementary filtered plankton added to the aquarium only survived for four days and did not moult to a second zoea.

The first zoeal stage of the red crab measured approximately 2 mm in length from the carapace (excluding dorsal spine) to the end of the furcae, had lateral spines on the carapace and a furcated telson with three pairs of inner setae. Exospines developed on the larger zoea larvae.

The standard error for dorsal spine to body width ratio was low in the reared red crab zoea, n=32 (Figure 4). Measurements of the dorsal spine to body width ratio from the selection of zoea from the monthly plankton samples revealed a wide scatter indicating that there were zoea of many crab species in the samples. Zoea that had a similar dorsal spine to body width ratio to that of the reared land crabs were found in December 2005 and February, April, September and October 2006.

Discussion

The plankton concentration in the waters around Christmas Island was highest in September 2006 at the end of the south-east monsoon when the sea surface temperature was lowest. The South Equatorial Current is strongest in this region towards the end of the south-east monsoon when the wind stress over the region is strongest (Meyers *et al.* 1995; Donguy & Meyers 1995).
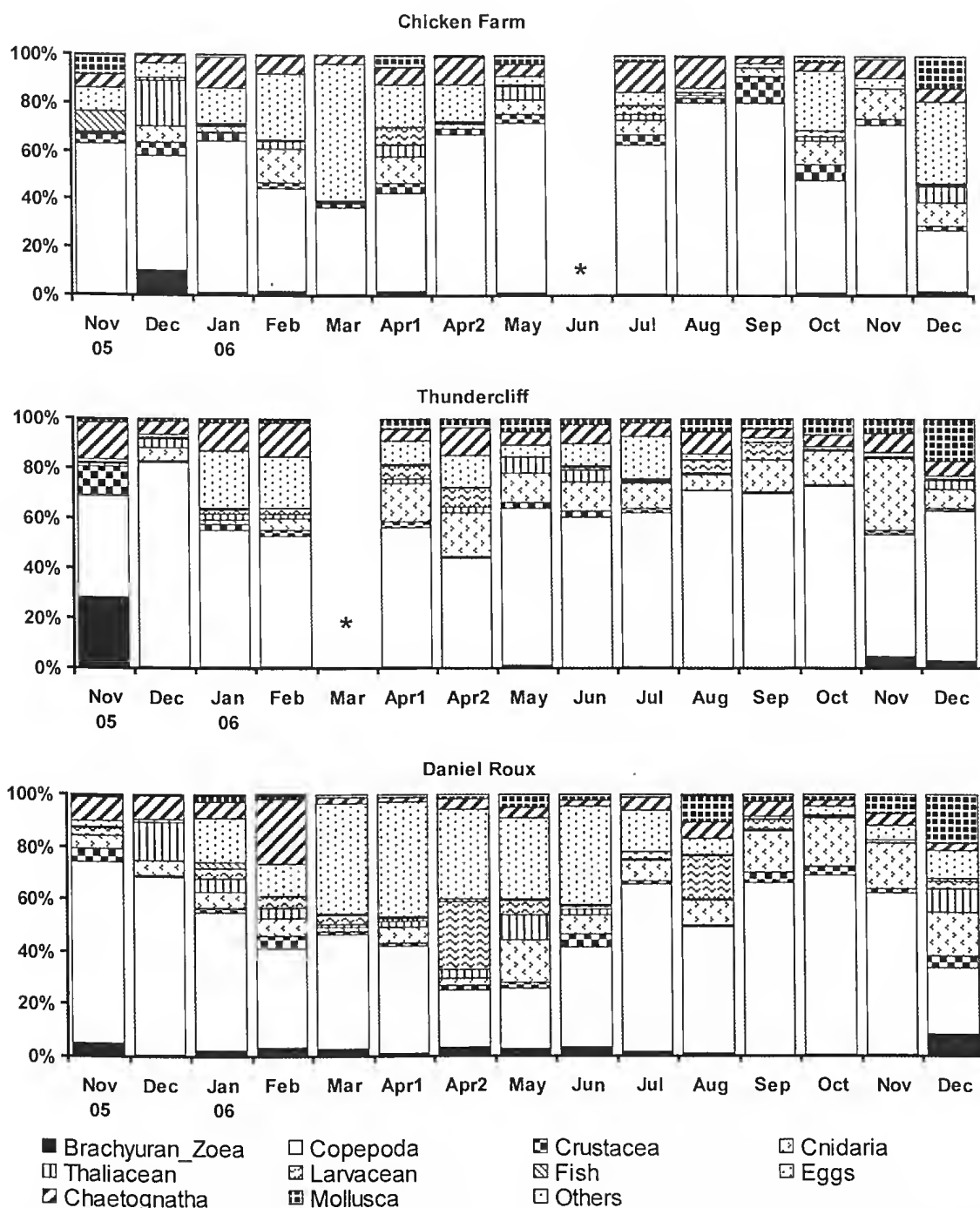
Figure 3. The monthly composition of the zooplankton sampled at three sites on Christmas Island, November 2005 – December 2006. * indicates that no samples were taken at Thundercliff in March 2006 or Chicken Farm in June 2006.

Upwelling on the northern flank of the South Equatorial Current has been linked to the increase in plankton concentration (Wyrtki 1962). During the Indian Ocean Expedition, Tranter & Kerr (1977) found that plankton concentration increased in the Eastern Indian Ocean at the end of the south-east monsoon and they ascribed this to increased productivity from the upwelling along the flank of the South Equatorial Current (Wyrtki 1962) or simply due to horizontal water movements (Tranter 1967).

The plankton concentration was consistently low from January, in the north-west monsoon, until July 2006

when the south-east monsoon strengthened. The low plankton concentration found when the South Equatorial Current is weak may reflect a return to the prevailing plankton impoverished waters of the South Indian Ocean gyre (Tranter & Kerr 1977).

This may infer that much of the recruitment at Christmas Island is from external sources dependent on the South Equatorial Current. This would be supported by the fish fauna which is typical of the Indo West Pacific region (Allen 2000) and by a low diversity of benthic invertebrates such as corals, molluscs and echinoderms (Done & Marsh 2000, Marsh 2000, Wells & Slack-Smith
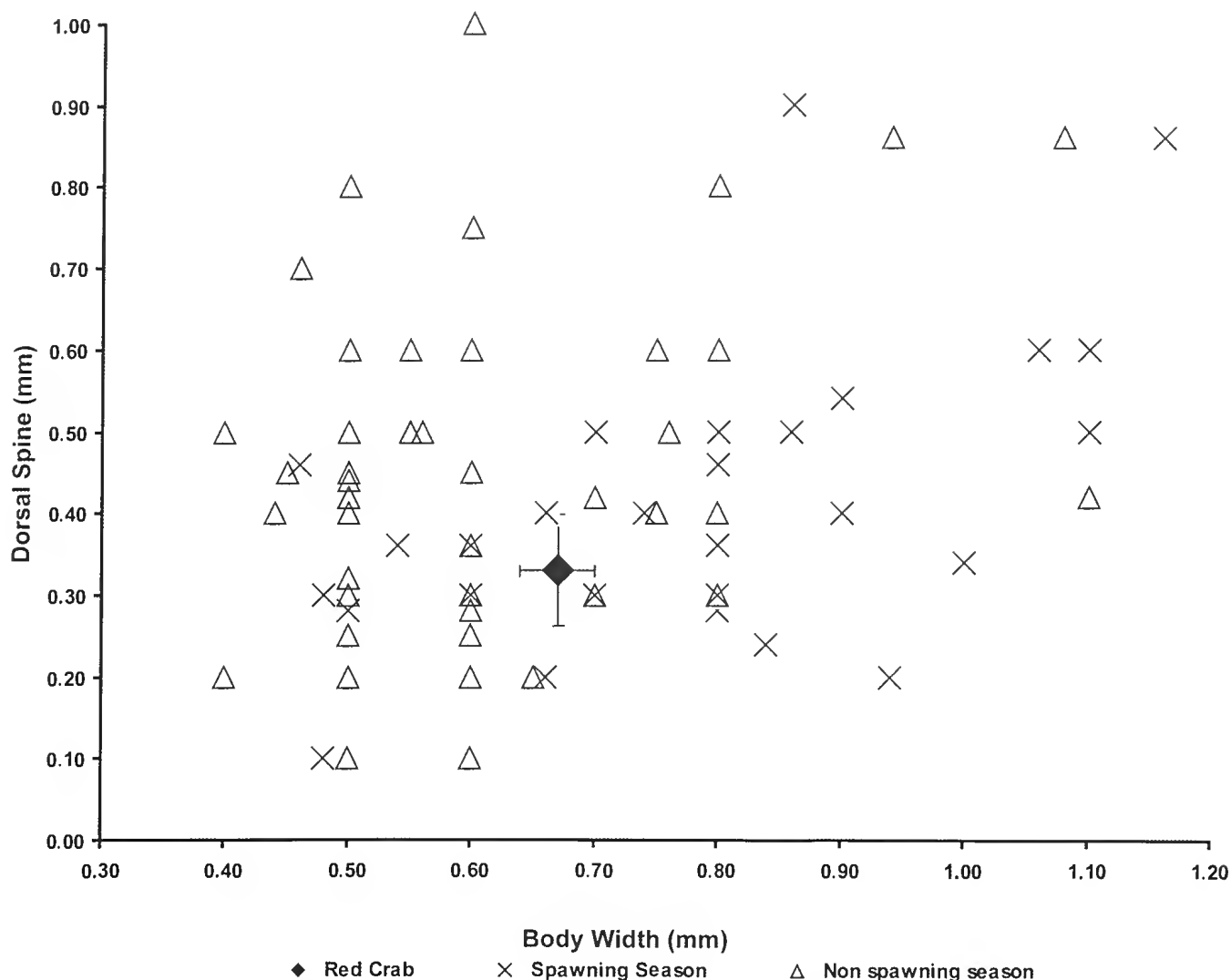
Figure 4. The relationship between the length of dorsal spine to body width for reared red crab zoea larvae (with SE bars) compared to those of a monthly selection of zoea collected in the plankton samples at Christmas Island. Note that two outlying data points of crabs with extended dorsal spines (1.6 mm) were omitted from the graph.

2000) as the pelagic larval duration of many species is not long enough for transport from neighbouring Indonesian or Australian populations.

The plankton concentrations at the three sites were significantly different throughout the sampling period. This difference may be explained by the bathymetry and conditions at the three sites. The Thundercliff and Daniel Roux sites both have little fringing reef and steep drop offs although the Daniel Roux site is more sheltered from the prevailing currents. The Chicken Farm site, in a small embayment on the north-east side of the island, has a wider fringing reef extending up to 50 m offshore and is more exposed to strong currents.

The concentrations of plankton caught at Christmas Island were low when compared to plankton studies in other coastal tropical areas (Nair *et al.* 1981; McKinnon *et al.* 2005). This can partly be explained by the use of a 500 μm mesh net which did not retain smaller plankton and also the location of Christmas Island in tropical, oceanic waters where plankton concentrations are

expected to be lower (Nair *et al.* 1981). The oceanic nature of the plankton sampled at Christmas Island was highlighted by presence of taxa such as hyperiid amphipods, euphausiids and salps (Gibbons 2000).

Over the sampling period, copepods were the most abundant component of the plankton accounting for 54 % of the individuals counted per m³ of water sampled at Christmas Island. This is lower than the value of 74 % for the tropical Indian Ocean determined by Longhurst (1985) from analysis of 4000 global plankton samples. However, his review was of studies which sampled with nets of 200– 300 μm mesh, finer than our 500 μm mesh net.

Brachyuran zoea were found in almost every plankton sample over the project duration. Surprisingly, the highest concentrations occurred in the samples collected in early November 2005, before the first red crab spawning later that month. This suggests that at least one other brachyuran crab species was spawning at that time. It was originally hypothesised that large numbers

of red crab larvae would be present in the plankton during the spawning season. However, this was not the case. Sporadic, lower than average rainfall over the 2005–2006 north-west monsoon resulted in only three small migrations, rather than one large migration, producing less crab larvae and identification of the zoea could not be inferred through high abundance levels.

Many of the 142 marine brachyuran crab species recorded from Christmas Island (Morgan 2000) have undescribed larval stages so to confirm the presence of red crab zoea in the plankton we compared those raised in the aquarium to those caught in the samples. There was a large variety of zoea in the plankton samples and some matched the morphometrics of the reared red crab zoea. However, some of the matching zoea occurred during months outside of the red crab spawning season indicating that the measured morphometrics do not provide conclusive identification. Chromatophores are recognised as the best way to positively identify brachyuran zoea as they do not change with growth, but they do fade with preservation (Boltovskoy 1999; Shanks 2001). Unfortunately, the chromatophores of the reared red crab larvae faded rapidly on preservation and hence could not be used for identification purposes.

The highest plankton concentrations, and potentially recruitment from external sources, coincided with the strongest westward flow of the South Equatorial current. Conversely, the red crabs spawned when the South Equatorial Current had weakened and westward transport was lowest. It is unknown where the red crab larvae develop. Based on observations that the highest returns of juvenile crabs occur in areas where the fringing reef is widest it has been suggested that they stay close to shore (Gray 1981). At Chicken Farm, where the fringing reef is wide, spawning crabs were observed in November and December 2005 and January 2006. A maximum of 6 crab zoea/m³ was recorded in December, four days after a spawning and 0.3 zoea/m³ in January and February, seven to nine days after spawning events. However, no subsequent juvenile returns were observed at this site (pers. obs. C. Davies). Although the red crab migrations were relatively small in 2005–2006, many million eggs would have been released over each spawning period and higher concentrations would have been expected in the samples if the zoea had remained inshore.

The larvae of many other crab species are known to develop offshore. For example, the blue crab, *Callinectes sapidu*, spawns in estuaries off the mid Atlantic coast of America and the larvae are immediately carried out into the open ocean where they develop in the surface waters (Johnson *et al.* 1984; Epifanio 1995). Blue crab recruitment is also sporadic but wind stress has been shown to be very important for successful recruitment with wind-driven onshore currents responsible for retaining the larvae in the general area and then returning the megalopae to the coast (Johnson *et al.* 1984; Garvine *et al.* 1997; Perry *et al.* 2003). Brachyuran crab larvae have also demonstrated active vertical movement to accomplish horizontal transport towards the shore (Cronin 1986; Blackmon & Eggleston 2001; Lee *et al.* 2005).

Whilst inshore development was not ruled out by this study, we suggest that red crab larvae might develop further offshore than previously thought, and that recruitment is dependent on oceanographic conditions being favourable for the return of megalopae to the island. The irregular recruitment of juvenile red crabs to Christmas Island, noted as once or twice a decade by Clark (1994), and the absence of high numbers of red crab zoea in the plankton during this study would support this hypothesis. Detailed exploration of the oceanography, in particular, eddy fields and lee effects from the island would probably be necessary to unravel the larval ecology of red crabs during their obligate marine phase.

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